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RESEARCH ARTICLES
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SYSTEMATIC POSITION AND CONSERVATION ASPECTS OF *MELINAEA MNASIAS THERA* (LEPIDOPTERA: NYMPHALIDAE: DANAINAE)

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The tribe Ithomiini (Nymphalidae: Danainae) includes nearly 400 species of butterflies distributed from Mexico to Northern Argentina, and adults of all species are aposematic and the main models in several Neotropical mimicry rings. The subtribe Melinaeina, a small group composed of five genera of large ithomiines, is the sister group of all remaining groups in the tribe Ithomiini. With 14 recognised species, the genus *Melinaea* is the most species rich, and also the most widespread within the Melinaeina. From all species of the genus, *Melinaea mnasias* is considered very rare and a little known one. This is also true for *Melinaea mnasias thera*, a subspecies from the Atlantic Forest with less than 20 specimens known in all world museums. Studies combining systematics, ecology, biogeography and natural history are priority in tropical areas, especially when focusing on threatened species. Thus, the aim of this study was to compile all available knowledge on the threatened *M. mnasias thera*, providing information to future management plans focusing on the conservation of this butterfly and its habitats. Data were compiled from scientific collections and personal observations, and the systematics of species of *Melinaea* was assessed by DNA sampling and analysis. The obtained phylogeny recovered the subtribe Melinaeina organised in two clades, the first composed by *Olyras* + *Paititia* and the second by *Eutresis* + (*Athyrtis* + *Melinaea*). *Melinaea mnasias thera* was recovered as a sister to *M. mnasias lucifer*. A total of only 17 specimens of *M. mnasias thera* from four Brazilian localities were found in all revised collections. However, well-preserved forests are present only at one of these localities, in the southern Bahia state, from where a recent specimen has been collected, suggesting that the last populations of *M. mnasias thera* are restricted to this region. If this is true, the real conservation status of this species could be much more critical than the estimated.

Key words: Atlantic Forest, Brazil, butterfly, Ithomiini, endangered species

Introduction

The tribe Ithomiini (Lepidoptera: Nymphalidae: Danainae) includes about 400 butterfly species distributed from Mexico to Northern Argentina (Doré et al., 2023). Adults of all species are aposematic and considered the main models in many Neotropical mimicry rings (Brown & Benson, 1974; Beccaloni, 1997). In a study combining morphological and molecular data, Brower et al. (2014) recovered the tribe Ithomiini divided in ten subtribes, nine of which are well supported by both types of characters, a result congruent with subsequent molecular studies (Garzón-Orduña et al., 2015; Chazot et al., 2019). The subtribe Melinaeina is composed of five genera of large ithomiines and was recovered as a sister group of all remaining ithomiines in the listed above studies. With 14 recognised species, the genus *Melinaea* Hübner, 1816 is the most species rich, and also the most widespread within the Melinaeina (Brown, 1979; McClure et al., 2018). From those 14 species, only three taxa occur in the Atlantic Forest, namely the endemic *Melinaea ethra* (Godart, 1819) and two subspecies of two widely distributed species, namely *Melinaea ludovica paraiya* Reakirt, 1866 and *Melinaea mnasias thera* C. Felder & R. Felder, 1865 (Brown, 1979).

Melinaea mnasias (Hewitson, [1856]) is divided into 11 described subspecies, and it is considered very rare and little known (Brown, 1977). Except for *M. mnasias comma* W. Forbes, 1927 and *M. mnasias lucifer* H. Bates, 1862, which are locally common, all other subspecies are scarce in collections. This is also true for the Atlantic Forest subspecies *Melinaea mnasias thera*, known from only 17 specimens so far (Brown & Freitas, 2008; Freitas et al., 2018; Rosa et al., 2023).

Melinaea mnasias thera occurs in a narrow region of the coastal Atlantic Forest in the Brazilian state of Bahia, at only two localities. Accordingly, this taxon was included in the Brazilian Red List, being assessed as «Critically Endangered» (CR) (MMA, 2003, 2014, 2022; Freitas et al., 2018). The compiling of all available information on any threatened butterflies is an important task, especially for the species which are scarce in museum collections (Freitas & Marini-Filho, 2011). In this specific case, *M. mnasias thera* occurs in a critical portion of the Atlantic Forest, a global biodiversity hotspot for conservation (Myers et al., 2000). Thus, the aim of this study was to investigate the systematic position of *M. mnasias thera*, its conservation aspects, and compile all available information about this rare butterfly. Studies combining systematics, ecology, biogeography and natural history are priority in tropical areas, especially when focusing on threatened species. Moreover, the information obtained for a given group of herbivores can be useful in studies of diversity and health of a given plant assemblage (Gilbert, 1980; Freitas, 1996). Finally, studies like this one are important for providing information to future management plans focusing on the conservation of threatened butterflies and their habitats.

Material and Methods

Specimens of *M. mnasias thera* (Fig. 1a) were found in the following nine public collections: Coleção Entomológica do Instituto Oswaldo Cruz, Instituto Oswaldo Cruz, Rio de Janeiro, Rio de Janeiro, Brazil (CEIOC); Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Paraná, Brazil (DZUP); Muséum National d'Histoire Naturelle, Paris, França (MNHN); Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM); Museu de Zoologia, Universidade de São Paulo, São Paulo, São Paulo, Brazil (MZUSP); Natural History Museum, London, England, United Kingdom (NHMUK); Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (MNRJ) (these specimens were lost by the fire that destroyed the Museum in 2018); Museum für Naturkunde, Berlin, Germany (ZMB); Zoological Collection, Museu de Diversidade Biológica da Universidade Estadual de Campinas, Campinas, São Paulo, Brazil (ZUEC). The search for data on *M. mnasias thera* followed the same databases and methods described in Rosa et al. (2023). Data labels of all specimens were compiled; they are available in Table S1.

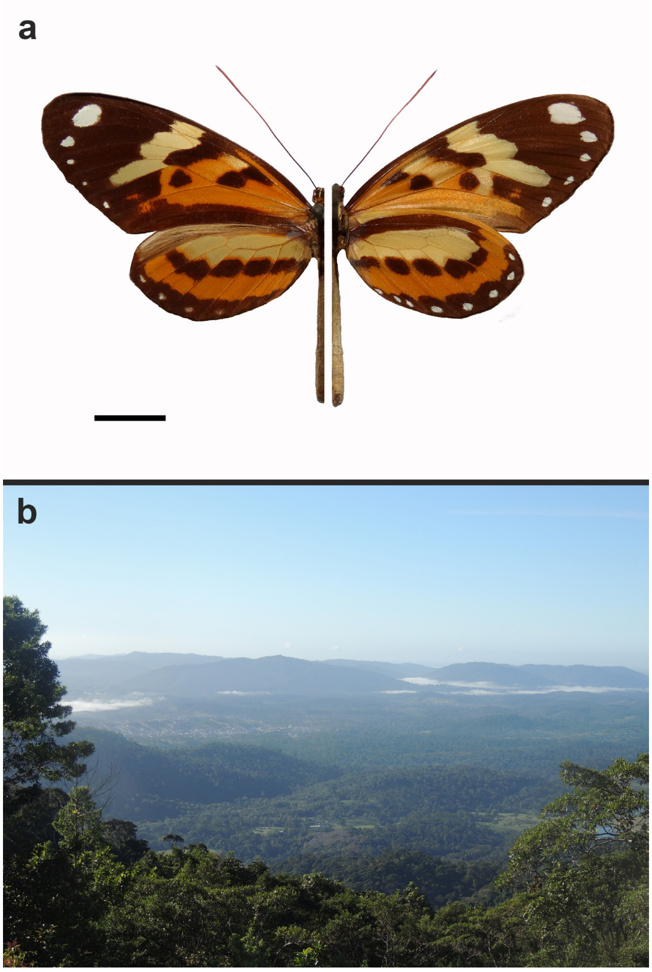

Fig. 1. Adult specimen and the habitat of *Melinaea mnasias thera*. Designations: A – *Melinaea mnasias thera* (left – dorsal view, right – ventral view); B – general view of forest habitats in Serra Bonita, Camacan, Bahia state, Brazil.

DNA sampling and analysis

All sequences used were downloaded from Genbank, except for the museum samples EB19-049 (MNHN, Muséum National d'Histoire Naturelle, Paris, France) and AHBR119 (ZUEC, Zoological Collection, Museu de Diversidade Biológica da Universidade Estadual de Campinas, Campinas, Brazil), which had their genomic DNA extracted from two legs using the QIAamp DNA MicroKit (QIAGEN®, USA) protocol, adapted with columns from MinElute PCR Purification Kit (QIAGEN®, Düsseldorf, Germany). The whole genome shotgun sequencing was performed on the two DNA extractions of museum specimens, following protocols described in Twort et al. (2021), which were modified from protocols in Meyer & Kircher (2010). Briefly, DNA was first blunt-end repaired, after which custom-made indexed Illumina adapters were ligated. The library was then pooled with 59 other Lepidoptera specimens and run on the Illumina NovaSeq platform. Raw reads were checked with FASTQC v. 0.11.8 (Andrews, 2010), and reads were cleaned with Prinseq v. 0.20.4 (Schmieder & Edwards, 2011) and Trimmomatic v. 0.38 (Bolger et al., 2014). The genome was then *de novo* assembled with spAdes v. 3.13.0 (Bankevich et al., 2012) with a kmer value of 21. Orthologs of the five standard genes for Lepidoptera (COI, EF1-α, CAD, wingless and GAPDH) were identified from the fragmented genome assembly using MESPA v. 1.3 (Neethiraj et al., 2017). See Twort et al. (2021) for more detailed descriptions of the bioinformatic pipelines. For AHBR119, we were able to identify all five genes (COI, EF1-α, CAD, wingless and GAPDH). For EB19-049 we were only able to find COI. All sequences were aligned on CIPRES Science Gateway portal v. 3.1 (Miller et al., 2010) using MAFFT v. 7 (Katoh & Standley, 2013).

The final concatenated matrix comprised 37 specimens, representing most of *Melinaea* species and more close related genera, with a total of 4698 base pairs and five genes. The type species of all genera are represented in the final matrix. *Tellervo zoilus* (Fabricius, 1775) was used to root the tree (see Table S3 for voucher numbers). Analyses to find the best-fit substitution models and partition subsets for the dataset (see Table S2 for best model selected for each partition), using «merge» option, were done using ModelFinder (Kalyaanamoorthy et al., 2017) with edge-linked partition model + FreeRate heterogeneity in IQ-TREE v. 1.6.12 (Nguyen et al., 2015).

The maximum likelihood tree was inferred using ten likelihood searches in IQ-TREE v. 1.6.12. The support was calculated using the ultrafast bootstrap (UFBoot) (Hoang et al., 2018), with 2000 replications, in addition to assessing node support through 1000 replications of Shimodaira Hasegawa approximate Likelihood Ratio Test (SH-aLRT) (-alrt 1000) (Guindon et al., 2010; Hoang et al., 2018) and approximate Bayes branch test (aBayes; Anisimova et al., 2011).

Results

Systematic position

In the obtained phylogeny, the subtribe Melinaeina was organised in two clades, the first composed by *Olyras* + *Paititia* (type species: *Olyras crathis* E. Doubleday, 1847 and *Paititia neglecta* Lamas, 1979) and the second by *Eutresis* + (*Athyrtis* + *Melinaea*) (type species: *Eutresis hypereia* E. Doubleday, 1847, *Athyrtis mechanitis* C. Felder & R. Felder, 1862 and *Melinaea ludovica* (Cramer, 1780)). The genus *Melinaea* was recovered as monophyletic and divided in two major clades, the first composed by *Melinaea mnasias* + *Melinaea ludovica* and the second formed by *Melinaea ethra* as the sister taxon to a large clade composed by nine species of *Melinaea*. The two individuals of *Melinaea mnasias thera* clustered together forming a clade with strong support, sister to *M. mnasias lucifer* (Fig. 2).

General information and conservation aspects

A total of only 17 specimens of *M. mnasias thera* were found in nine public collections (Table S1). These specimens represent geographical records of four localities in the Brazilian states of Rio de Janeiro, Espírito Santo, and Bahia (records from the state of São Paulo, Paraguay and Colombia are mistakes, see Rosa et al., 2023) (see Table S1, Fig. 3). Most individuals of *M. mnasias thera* are either very old or without any information on collecting dates, and a single individual has been collected in the XXI century (in 2016, Table S1). Morphology (mostly wing pattern) was presented and discussed by Fox (1960), and Brown (1977) presented additional data on taxonomy and distribution, anticipating by a decade the presence of *M. mnasias* in coastal Bahia state.

Based on the trustworthy geographical data, *M. mnasias thera* occurs in lowland coastal forests (Fig. 1b), at altitudes of 100–400 m a.s.l. (Fig. 3). At both localities, where *M. mnasias thera* was reported in the Bahia state, at least half of the area is covered by cocoa plantations locally known as «cabruca», where the cocoa trees are planted in the shade of larger trees.

The known distribution of *M. mnasias thera* is disjunct. The two localities in Bahia state (Camacan and Itapebi) are relatively close to each other (about 60 km of distance), as well as the two localities in the Espírito Santo state (Alegre) and Rio de Janeiro state (Bom Jesus do Itabapoana) are about 50 km of distance to each other. These two pairs, however, have a large gap of about 700 km between them. Based on these data, the extent of occurrence (EOO) of *M. mnasias thera* was estimated as at 7264.35 km^2 and its area of occupancy (AOO) as 16 km^2 (Rosa et al., 2023).

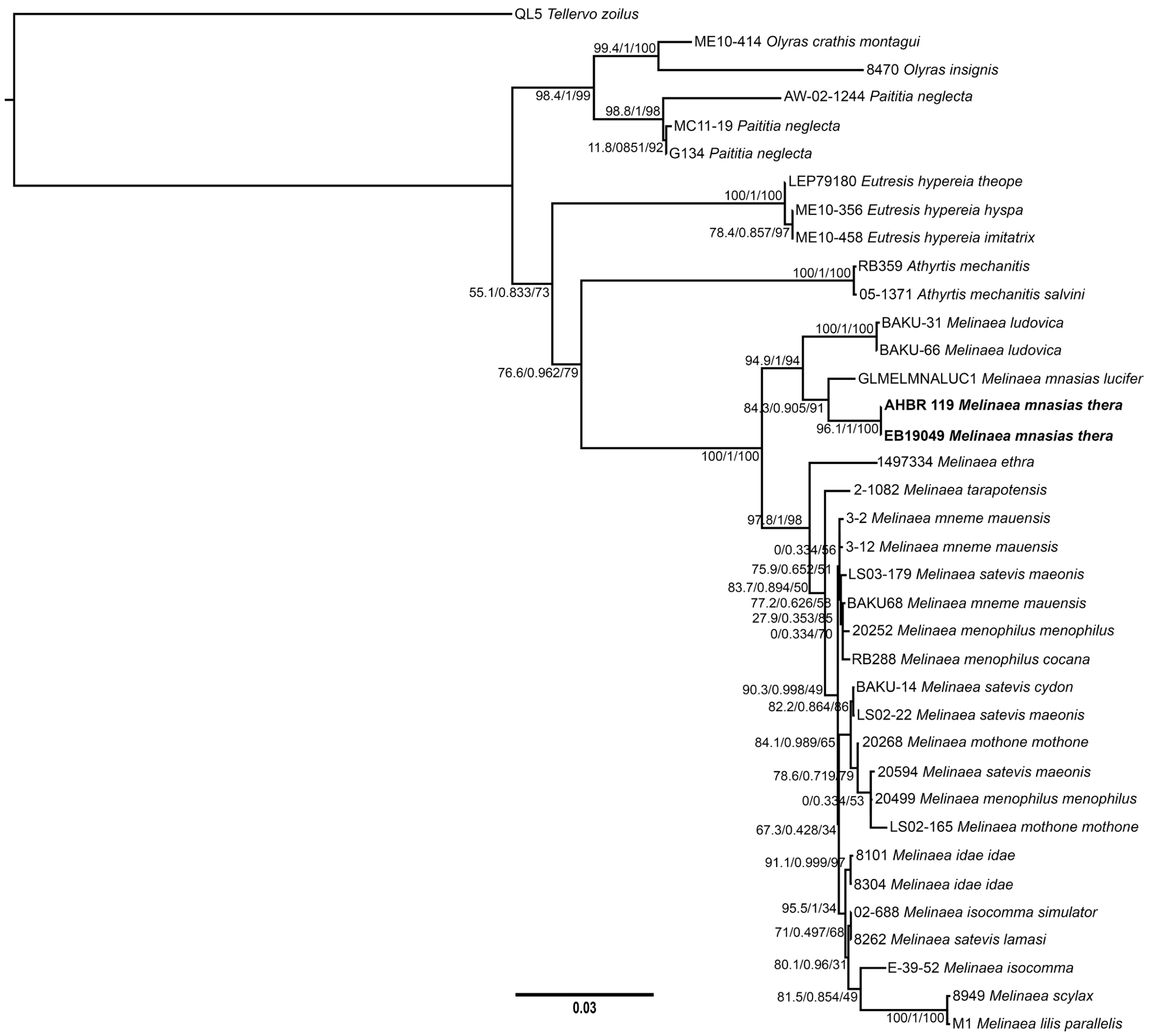

Fig. 2. Phylogenetic relationships of *Melinaea* species based on COI, EF1-α, CAD, wingless, and GAPDH genes and obtained by a maximum likelihood analysis. Numbers near the nodes are SH-aLRT/aBayes/Ultrafast bootstrap support values.

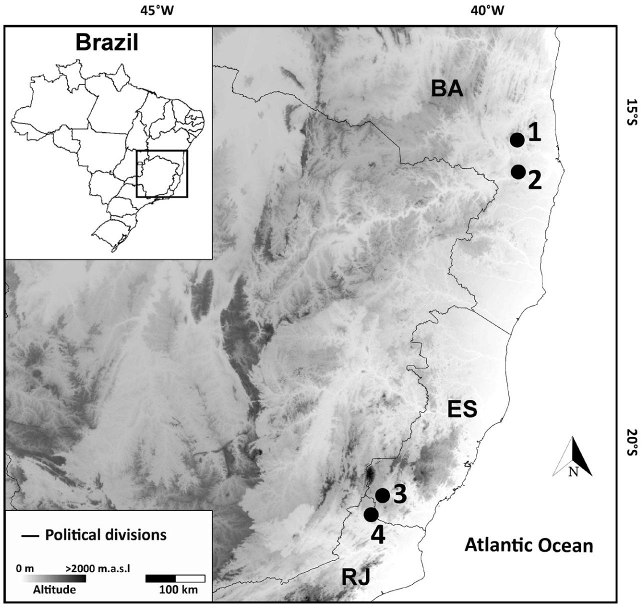

Fig. 3. Map showing the four known localities of *Melinaea mnasias thera*. Designations: 1 – Itapebi, Bahia state; 2 – Reserva Serra Bonita, Camacan, Bahia state; 3 – Alegre, Espírito Santo state; 4 – Bom Jesus de Itabapoana, Rio de Janeiro state.

Discussion

Phylogeny of subtribe Melinaeina and position of M. mnasias thera

Although composed of only five genera, the internal relationships of the subtribe Melinaeina has not reached a consensus based on previous studies. Common points include the monophyly of *Melinaea* and the clade formed by *Olyras* + *Paititia* (Brower et al., 2006, 2014; Willmott & Freitas, 2006; Garzón-Orduña et al., 2015; Chazot et al., 2019: Fig. S2.1, Fig. S2.2). The position of the genus *Athyrtis* is not congruent with previous studies. Although recent molecular studies recovered it as a sister group of all remaining Melinaeina (Garzón-Orduña et al., 2015; Chazot et al., 2019), the present study recovered *Athyrtis* as a sister group of *Melinaea*. This result is similar to that obtained in the morphological study by Willmott & Freitas (2006), in combined analyses by Brower et al. (2014), and in an early molecular study by Brower et al. (2006). In addition, together with *Melinaea*, *Athyrtis* is the only other genus of Melinaeina that presents a tiger wing pattern; *Olyras*, *Paititia* and *Eutresis* have translucent wing patterns. A second divergence is the position of *Eutresis*: in the present study it was the sister group of *Athyrtis* + *Melinaea*, while it is the sister to *Olyras* + *Paititia* in previous morphological and molecular studies (Willmott & Freitas, 2006; Chazot et al., 2019).

The systematic position of *Melinaea mnasias thera* confirms the placement of this taxon as a subspecies of *M. mnasias*, as proposed by Fox (1965) based on wing patterns. In addition, the present results show that *M. mnasias* is sister to *M. ludovica* (Cramer, 1780), contrasting with the results of Chazot et al. (2019: Fig. S2.1, Fig. S2.2), where *M. mnasias* was recovered as the sister group to other *Melinaea* species. The lack of resolution among the large clade composed by nine species of *Melinaea* confirm the results found by McClure & Elias (2017), and is a result of the absence of mitochondrial divergence, suggesting a recent radiation for these nine species.

Only three species of *Melinaea* are present in the Atlantic Forest. There are no discernible reasons why none of the remaining nine taxa have reached the Atlantic Forest, as many of them are extremely common, locally abundant and present in several forested habitats (Brown, 1977; Freitas, 1996). McClure & Elias (2017) suggested that these nine taxa could have originated from a recent and rapid radiation. In fact, the dating provided by Chazot et al. (2019: Fig. S2.2) showed that this clade originated about one million year ago, and most species are much younger than that. In this case, it is possible that these species just have not had enough time to reach and colonise the Atlantic Forest domain yet.

Geographical distribution and conservation

Based on the reliable data, *M. mnasias thera* has been reported from four localities from south Bahia to north Rio de Janeiro states (Fig. 3). However, it is important to call attention to two important factors. First, most of the forests in the northern Rio de Janeiro state and southern Espírito Santo state have been destroyed and persists as small remnants (MMA, 2000), and it is hard to believe that populations of *M. mnasias thera* are still present in this region. Second, not a single individual of *M. mnasias thera* has been collected or sighted in the last large forest remnants in the central and northern Espírito Santo state, including the low mountains near the municipality of Santa Teresa and the large tableland forests near the municipality of Linhares, both intensively censused in the last three decades (Brown & Freitas, 2000; Freitas et al., 2016). Accordingly, it is not impossible that the last populations of *M. mnasias thera* are restricted to the wet forests in south Bahia state. If this is true, the actual EOO should be much smaller than that presented in Rosa et al. (2023), and the estimate of EOO, which is now on the threshold to Vulnerable (VU) category, is much more optimistic than the reality. However, the fact that *M. mnasias thera* may persist in areas with cocoa plantation opens several possibilities for conservation, since there are still several areas where cocoa is cultivated in the «cabruca» system (Cocoa plantation shaded by native trees). The reasons for this can be explained in its biology. So, although the host plant and immature stages of *M. mnasias thera* are unknown, it likely uses *Dyssochroma* spp. (Solanaceae); the same host plants are used by the other two *Melinaea* in the Atlantic Forest (Brown, 1987; Drummond & Brown, 1987; Brown & Freitas, 1994). These plants are epiphytic, growing in tall trees near the canopy, exactly the trees that are preserved to provide the shade for the cocoa plantations in south Bahia state.

Based on this scenario, it is very important that potentially additional localities of populations of this rare butterfly should be surveyed. Suggested areas in the South Bahia state include the Serra das Lontras National Park and the region of Una Biological Reserve. In addition, the large areas of cocoa plantations in the Ilhéus-Itabuna region could harbour populations of *M. mnasias thera*. It should not be difficult to obtain eggs from wild caught females, as for other species of *Melinaea* (McClure & Elias, 2017; A.V.L. Freitas, unpublished). Details of its life cycle could provide clues to a better understanding of its rarity, as well as important information for conservation actions for this taxon.

Conclusions

The present study is the most complete concerning the threatened Brazilian butterfly *Melinaea mnasias thera*. This is one of the rarest and the most threatened *Melinaea* taxa, so far known from only 17 specimens deposited in nine museum collections. Most of the potential historical range of this species is now deforested. The species is presently restricted to the large forest remnants in the southern part of the Bahia state, in northeastern Brazil. In fact, given this scenario, only two localities are possibly maintaining populations of *M. mnasias thera*, meaning that the current IUCN status of Vulnerable could be much more optimistic than the reality. Additional populations should be located, as these would provide more opportunities for conservation of this rare butterfly.

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Supporting Information

Additional data for the paper of Rosa et al. (2024) may be found in the **Supporting Information**.

References

Andrews S. 2010. *FastQC: a quality control tool for high throughput sequence data*. Available from https://www.bioinformatics.babraham.ac.uk/projects/fastqc

Anisimova M., Gil M., Dufayard J.F., Dessimoz C., Gascuel O. 2011. Survey of branch support methods demonstrates accuracy, power, and robustness of fast likelihood-based approximation schemes. *Systematic Biology* 60(5): 685–699. DOI: 10.1093/sysbio/syr041

Bankevich A., Nurk S., Antipov D., Gurevich A.A., Dvorkin M., Kulikov A.S., Lesin V.M., Nikolenko S.I., Pham S., Prjibelski A.D., Pyshkin A.V., Sirotkin A.V., Vyahhi N., Tesler G., Alekseyev M.A., Pevzner P.A. 2012. SPAdes: A new genome assembly algorithm and its applications to single-cell sequencing. *Journal of Computational Biology* 19(5): 455–477. DOI: 10.1089/cmb.2012.0021

Beccaloni G.W. 1997. Ecology, natural history and behaviour of Ithomiine butterflies and their mimics in Ecuador (Lepidoptera: Nymphalidae: Ithomiinae). *Tropical Lepidoptera* 8(2): 103–124.

Bolger A.M., Lohse M., Usadel B. 2014. Trimmomatic: A flexible trimmer for Illumina sequence data. *Bioinformatics* 30(15): 2114–2120. DOI: 10.1093/bioinformatics/btu170

Brower A.V.Z., Freitas A.V.L., Lee M.M., Silva-Brandão K.L., Whinnett A., Willmott K.R. 2006. Phylogenetic relationships among the Ithomiini (Lepidoptera: Nymphalidae) inferred from one mitochondrial and two nuclear gene regions. *Systematic Entomology* 31(2): 288–301. DOI: 10.1111/j.1365-3113.2006.00321.x

Brower A.V.Z., Willmott K.R., Silva-Brandão K.L., Garzón-Orduña I.J., Freitas A.V.L. 2014. Phylogenetic relationships of ithomiine butterflies (Lepidoptera: Nymphalidae: Danainae) as implied by combined morphological and molecular data. *Systematics and Biodiversity* 12(2): 133–147. DOI: 10.1080/14772000.2014.899650

Brown K.S. 1977. Geographical patterns of evolution in Neotropical Lepidoptera: differentiation of the species of *Melinaea* and *Mechanitis* (Nymphalidae, Ithomiinae). *Systematic Entomology* 2(3): 161–197. DOI: 10.1111/j.1365-3113.1977.tb00368.x

Brown K.S. 1979. *Ecological Geography and Evolution in Neotropical Forests*. Livre Docência Thesis. Campinas: Universidade Estadual de Campinas. 109 p.

Brown K.S. 1987. Chemistry at the Solanaceae/Ithomiinae Interface. *Annals of the Missouri Botanical Garden* 74(2): 359–397. DOI: 10.2307/2399406

Brown K.S., Benson W.W. 1974. Adaptive polymorphism associated with multiple Müllerian mimicry in *Heliconius numata*. *Biotropica* 6(4): 205–228. DOI: 10.2307/2989666

Brown K.S., Freitas A.V.L. 1994. Juvenile stages of Ithomiinae: overview and systematics (Lepidoptera: Nymphalidae). *Tropical Lepidoptera* 5(1): 9–20.

Brown K.S., Freitas A.V.L. 2000. Diversidade de Lepidoptera em Santa Teresa, Espírito Santo. *Boletim do Museu de Biologia Mello Leitão (Nova Série)* 11/12: 71–116.

Brown K.S., Freitas A.V.L. 2008. *Melinaea mnasias thera* C. Felder & R. Felder, 1865. In: A.B.M. Machado, G.M. Drummond, A.P. Paglia (Eds.): *Livro Vermelho da Fauna Brasileira Ameaçada de Extinção*. Brasília, DF, Belo Horizonte, MG: Ministério do Meio Ambiente, Fundação Biodiversitas. P. 418.

Chazot N., Willmott K.R., Lamas G., Freitas A.V.L., Piron-Prunier F., Arias C.F., Mallet J., De-Silva D.L., Elias M. 2019. Renewed diversification following Miocene landscape turnover in a Neotropical butterfly radiation. *Global Ecology and Biogeography* 28(8): 1118–1132. DOI: 10.1111/geb.12919

Doré M., Willmott K.R., Lavergne S., Chazot N., Freitas A.V.L., Fontaine C., Elias M. 2023. Mutualistic interactions shape global spatial congruence and climatic niche evolution in Neotropical mimetic butterflies. *Ecology Letters* 26(6): 843–857. DOI: 10.1111/ele.14198

Drummond B.A., Brown K.S. 1987. Ithomiinae (Lepidoptera: Nymphalidae): summary of known larval food plants. *Annals of the Missouri Botanical Garden* 74(2): 341–358. DOI: 10.2307/2399405

Fox R.M. 1960. A monograph of the Ithomiidae (Lepidoptera). Part II. The tribe Melinaeini Clark. Transactions of the American Entomological Society 86(2): 109–171.

Fox R.M. 1965. Additional notes on *Melinaea* Hübner (Lepidoptera: Ithomiidae). Proceedings of the Royal Entomological Society of London. Series B, Taxonomy 34(7–8): 77–82. DOI: 10.1111/j.1365-3113.1965.tb01694.x

Freitas A.V.L. 1996. Population biology of *Heterosais edessa* (Nymphalidae) and its associated Atlantic Forest Ithomiinae community. *Journal of the Lepidopterists' Society* 50(4): 273–289.

Freitas A.V.L., Marini-Filho O.J. 2011. Plano de Ação Nacional para Conservação dos Lepidópteros Ameaçados de Extinção. Brasília: Instituto Chico Mendes de Conservação da Biodiversidade. 124 p.

Freitas A.V.L., Marini-Filho O.J., Mielke O.H.H., Casagrande M.M., Brown K.S., Kaminski L.A., Iserhard C.A., Ribeiro D.B., Dias F.M.S., Dolibaina D.R., Carneiro E., Uehara-Prado M., Romanowski H.P., Emery E.O., Accacio G.M., Rosa A.H.B., Bizarro J.M.S., Silva A.R.M., Guimarães M.P., Silva N.A.P., Braga L., Almeida G. 2018. *Melinaea mnasias thera* C. Felder & R. Felder, 1865. In: *Livro Vermelho da Fauna Brasileira Ameaçada de Extinção*. Vol. 7: Invertebrados. Brasília: ICMBio. P. 137–139.

Freitas A.V.L., Brown K.S., Mielke O.H.H., Santos J.P., Vasconcellos-Neto J. 2016. Borboletas da Reserva Natural Vale, Linhares/ES. In: S.G. Rolim, L.F.T. Menezes, A.C. Srbek-Araujo (Eds.): *Floresta Atlântica de Tabuleiro: Diversidade e Endemismos na Reserva Natural Vale*. Belo Horizonte: Editora Rupestre. P. 317–328.

Garzón-Orduña I.J., Silva-Brandão K.L., Willmott K.R., Freitas A.V.L., Brower A.V.Z. 2015. Incompatible ages for clearwing butterflies based on alternative secondary calibrations. *Systematic Biology* 64(5): 752–767. DOI: 10.1093/sysbio/syv032

Gilbert L.E. 1980. Food web organization and the conservation of neotropical diversity. In: M.E. Soule, B.A. Wilcox (Eds.): *Conservation of neotropical biology: an evolutionary-ecological perspective*. Sunderland (MA): Sinauer. P. 11–33.

Guindon S., Dufayard J.F., Lefort V., Anisimova M., Hordijk W., Gascuel O. 2010. New Algorithms and Methods to Estimate Maximum-Likelihood Phylogenies: Assessing the Performance of PhyML 3.0. *Systematic Biology* 59(3): 307–321. DOI: 10.1093/sysbio/syq010

Hoang D.T., Chernomor O., von Haeseler A., Minh B.Q., Vinh L.S. 2018. UFBoot2: Improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution* 35(2): 518–522. DOI: 10.1093/molbev/msx281

Kalyaanamoorthy S., Minh B.Q., Wong T.K.F., von Haeseler A., Jermiin L.S. 2017. ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nature Methods* 14(6): 587–589. DOI: 10.1038/nmeth.4285

Katoh K., Standley D.M. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30(4): 772–780. DOI: 10.1093/molbev/mst010

McClure M., Dutrillaux B., Dutrillaux A.M., Lukhtanov V., Elias M. 2018. Heterozygosity and Chain Multivalents during Meiosis Illustrate Ongoing Evolution as a Result of Multiple Holokinetic Chromosome Fusions in the Genus *Melinaea* (Lepidoptera, Nymphalidae). *Cytogenetic and Genome Research* 153(4): 213–222. DOI: 10.1159/000487107

McClure M., Elias M. 2017. Ecology, life history, and genetic differentiation in Neotropical *Melinaea* (Nymphalidae: Ithomiini) butterflies from north-eastern Peru. *Zoological Journal of the Linnean Society* 179(1): 110–124. DOI: 10.1111/zoj.12433

Meyer M., Kircher M. 2010. Illumina sequencing library preparation for highly multiplexed target capture and sequencing. *Cold Spring Harbor Protocols* 2010(6): pdb.prot5448. DOI: 10.1101/pdb.prot5448

Miller M.A., Pfeiffer W., Schwarts T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: *2010 Gateway Computing Environments Workshop*. New Orleans, Louisiana, USA. P. 1–8. DOI: 10.1109/GCE.2010.5676129

MMA. 2003. *Instrução Normativa №003 de 28 de maio de 2003*. Diário Oficial da União, Brasília. DF, Seção 1:88.

MMA. 2014. *Lista Nacional Oficial de Espécies da Fauna Ameaçadas de Extinção – Anexo I à Portaria №444, de 17 de dezembro de 2014*. Diário Oficial da União, Brasília, DF. Seção 1. Vol. 245: 121–126.

MMA. 2022. *Portaria MMA №148, de 7 de Junho de 2022 – Atualiza o teor do Anexo da Portaria №443, de 17 de dezembro de 2014, Lista oficial de espécies da flora brasileira ameaçadas de extinção*. Diário Oficial da União, Brasília, DF. Seção 1, 108:74.

MMA. 2000. *Avaliação e ações prioritárias para a conservação da biodiversidade da Mata Atlântica e Campos Sulinos*. Brasília: MMA/SBF. 40 p.

Myers N., Mittermeier R.A., Mittermeier C.G., Fonseca G.A.B., Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403(6772): 853–858. DOI: 10.1038/35002501

Neethiraj R., Hornett E.A., Hill J.A., Wheat C.W. 2017. Investigating the genomic basis of discrete phenotypes using a Pool-Seq-only approach: New insights into the genetics underlying colour variation in diverse taxa. *Molecular Ecology* 26(19): 4990–5002. DOI: 10.1111/mec.14205

Nguyen L.T., Schmidt H.A., von Haeseler A., Minh B.Q. 2015. IQ-TREE: A Fast and Effective Stochastic Algorithm for Estimating Maximum-Likelihood Phylogenies. *Molecular Biology and Evolution* 32(1): 268–274. DOI: 10.1093/molbev/msu300

Rosa A.H.B., Ribeiro D.B., Freitas A.V.L. 2023. How data curation and new geographical records can change the conservation status of threatened Brazilian butterflies. *Journal of Insect Conservation* 27(3): 403–414. DOI: 10.1007/s10841-023-00464-0

Schmieder R., Edwards R. 2011. Quality control and preprocessing of metagenomic datasets. *Bioinformatics* 27(6): 863–864. DOI: 10.1093/bioinformatics/btr026

Twort V.G., Minet J., Wheat C.W., Wahlberg N. 2021. Museomics of a rare taxon: placing Whalleyanidae in the Lepidoptera Tree of Life. *Systematic Entomology* 46(4): 926–937. DOI: 10.1111/syen.12503

Willmott K.R., Freitas A.V.L. 2006. Higher-level phylogeny of the Ithomiinae (Lepidoptera: Nymphalidae): classification, patterns of larval hostplant colonization and diversification. *Cladistics* 22(4): 297–368. DOI: 10.1111/j.1096-0031.2006.00108.x

СИСТЕМАТИЧЕСКОЕ ПОЛОЖЕНИЕ И ПРИРОДООХРАННЫЕ АСПЕКТЫ *MELINAEA MNASIAS THERA* (LEPIDOPTERA: NYMPHALIDAE: DANAINAE)

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Триба Ithomiini (Nymphalidae: Danainae) включает около 400 видов чешуекрылых, распространенных от Мексики до Северной Аргентины. При этом взрослые особи всех видов являются апосематическими и выступают основными моделями в нескольких кольцах неотропической мимикрии. Небольшая подтриба Melinaeina, состоящая из пяти родов крупных чешуекрылых, является сестринской группой всех остальных групп трибы Ithomiini. Род *Melinaea*, насчитывающий 14 видов, является самым крупным, а также самым распространенным в пределах подтрибы Melinaeina. Из всех видов рода *Melinaea mnasias* считается очень редким и малоизученным. Это справедливо и для *Melinaea mnasias thera*, подвида из Атлантического леса, менее 20 экземпляров которого известно во всех музеях мира. Исследования, сочетающие систематику, экологию, биогеографию и естественную историю, являются приоритетными в тропических регионах, особенно когда основное внимание уделяется видам, находящимся под угрозой исчезновения. В связи с этим целью этого исследования было собрать все доступные данные о *M. mnasias thera*, находящемся под угрозой исчезновения, предоставив информацию для будущих планов управления, направленных на сохранение этой бабочки и ее среды обитания. Информация была собрана на основе научных коллекций и личных наблюдений, а систематика видов *Melinaea* оценена путем отбора и анализа ДНК. Полученные данные о филогении восстановили подтрибу Melinaeina, организованную в две клады: первую составляют *Olyras* + *Paititia*, а вторую – *Eutresis* + (*Athyrtis* + *Melinaea*). *Melinaea mnasias thera* был обнаружен как сестринский подвид к *M. mnasias lucifer*. Всего во всех изученных коллекциях обнаружено 17 экземпляров *M. mnasias thera* из четырех местонахождений в Бразилии. Однако хорошо сохранившиеся леса присутствуют только в одном из этих мест, на юге штата Баия, откуда недавно был собран экземпляр. Это позволяет предположить, что последние популяции *M. mnasias thera* ограничены этим регионом. Если это действительно так, то реальный природоохранный статус этого таксона может быть гораздо более критичным, чем предполагалось.

Ключевые слова: Ithomiini, атлантический лес, бабочка, Бразилия, исчезающий вид

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МНОГОЛЕТНИЙ ДИСТАНЦИОННЫЙ МОНИТОРИНГ ЛЕЖБИЩА *EUMETOPIAS JUBATUS* (PINNIPEDIA, OTARIIDAE) НА ОСТРОВЕ МАТЫКИЛЬ В ЗАПОВЕДНИКЕ «МАГАДАНСКИЙ» (РОССИЯ)

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Резкое сокращение численности *Eumetopias jubatus* (далее – сивуч) почти по всему ареалу привело к необходимости организации мониторинга состояния данного вида. На территории России подобная работа была организована с начала 2000-х гг. и включает в себя наблюдения за численностью сивуча, мечение новорожденных детенышей и слежение за их выживаемостью, миграциями и размножением на протяжении их жизни. В первое десятилетие исследований сбор данных о численности сивуча и встречах тавреных животных проводился в летний период наблюдателями, находящимися непосредственно на лежбищах. С 2011 г. на многих лежбищах начали устанавливать специально сконструированные и самостоятельно изготовленные автономные фоторегистраторы, которые вели круглогодичную съемку лежбищ. В 2013 г. шесть фотосистем было размещено в государственном природном заповеднике «Магаданский» на репродуктивном лежбище сивуча на острове Матыкиль. Камеры вели съемку в интервале 5–30 мин. Обслуживание фоторегистраторов проводилось один раз в год. За восемь лет работы было получено 721 927 фотографий; из них 60 632 фотографии были проанализированы. Было установлено, что сивучи используют лежбище на протяжение всего года за исключением марта, что связано с образованием сплошного ледяного покрова в районе лежбища острова Матыкиль, который препятствует выходу животных на берег. В течение года отмечено два пика численности сивуча: летний и, более многочисленный, осенний. В летний период на лежбище преобладают самки, в осенне-зимний – молодые животные (преимущественно самцы) и самцы-секачи. Зимой их численность на берегу невысока. На острове Матыкиль можно встретить сивучей со всех репродуктивных лежбищ Дальнего Востока, за исключением животных, родившихся на Командорских островах. Наибольшее число сивучей-мигрантов появляется в осенний период и представлено преимущественно молодыми животными (возраст 1–3 года) и полусекачами (молодые самцы возраста 4–7 лет). В целом, данные, полученные с помощью автономных фоторегистраторов, позволяют получить детальную картину использования лежбища сивучами в течение всего годового цикла жизни, проследить сезонную динамику численности, половозрастной состав особей на берегу и репродуктивный успех меченных животных. В настоящее время применение автономных автоматических фоторегистраторов остается единственным доступным методом круглогодичного мониторинга за состоянием труднодоступных и удаленных лежбищ сивуча.

Ключевые слова: меченные животные, сезонная динамика, сивуч, учеты, фоторегистратор, численность, тавро, Ямские острова

Введение

С 1970-х гг. численность *Eumetopias jubatus* Schreber, 1776 (далее – сивуч) начала резко снижаться на всем ареале обитания. К концу 1980-х гг. она сократилась более чем на 60%, с 300 000 особей в 1960-х гг. до 116 000 в 1989 г. (Loughlin et al., 1992). Азиатская популяция сивуча в середине XIX в. составляла около 115 000 особей, а к концу 1990-х гг. численность снизилась до 13 000 особей (Burkanov & Loughlin, 2005). С 1994 г. сивуч внесен в Красную книгу Российской Федерации (2021). Для организации охраны вида необходимы регулярные данные о состоянии его численности, что обуславливает необходимость ежегодного мониторинга сивуча.

С начала 2000-х гг. в рамках программы по изучению азиатской популяции сивуча и выявлению причин спада его численности на территории России ведется регулярный мониторинг лежбищ, включающий слежение за численностью особей, мечение детенышей методом горячего тавления и наблюдения за миграциями и размножением меченых тюленей. Сбор данных проводился наблюдателями в летний период. Однако ввиду логистических трудностей при организации экспедиций и опасности работы наблюдателей на удаленных островах нами было найдено решение о внедрении автоматических фоторегистраторов, способных работать автономно без присутствия людей в течение года и получать большую часть важной информации в результате анализа фотографий. Похожие фотосистемы были ранее разработаны и успешно использовались для дистанционного мониторинга численности сивуча (Kulinchenko et al., 2004; Marcotte, 2006), *Odobenus rosmarus divergens* Illiger, 1811 (Holt, 2019), и *Phoca vitulina richardii* Gray, 1864 (Boveng et al., 2011) на Аляске. В 2011 г. на Дальнем Востоке России были установлены автономные автоматические фоторегистраторы на лежбищах сивуча на острове Медный (Командорские острова), мысах Козлова и Кекурный (полуостров Камчатка), острове Шиашкотан (Курильские острова) (Алтухов и др., 2011). В 2012 г. фотосистемы уже функционировали на десяти лежбищах сивучей (Бурканов и др., 2015). На острове Матыкиль (Ямские острова) мониторинг лежбища сивуча, включающий мечение, наблюдение за мечеными особями и учет численности, ведется с 2000 г. Но из-за труднодоступности острова Матыкиль и крайне сложных условий проживания на нем лишь в отдельные годы проводились краткосрочные наблюдения продолжительностью в несколько недель (Задальский, 2000; Burkanov & Loughlin, 2005; Грачев, Бурканов, 2015). В 2013 г. здесь были установлены фоторегистраторы, позволившие осуществлять круглогодичный сбор данных. Целью настоящего исследования является оценка характера использования лежбища сивучами в течение года на основе данных, полученных с использованием фоторегистраторов. Основными задачами работы было установить сроки подхода животных, их численность в течение года, половой и возрастной состав, состав животных по своему происхождению.

Материал и методы

Остров Матыкиль (59.326389° N, 155.543611° E) входит в состав Ямского архипелага, расположенного в северной части Охотского моря у входа в залив Шелихова и является островной частью Ямского участка заповедника «Магаданский» (рис. 1). Ширина пролива, отделяющего остров Матыкиль от материковой части (мыс Пьягина, самая восточная точка полуострова Пьягина), составляет 16.3 км. Остров Матыкиль представляет собой скалистый кряж, протяженностью по осевому гребню 5.5 км, шириной в срединной части до 2.0 км, максимальной высотой 695 м н.у.м. Проективная площадь острова Матыкиль – 6.2 км^2. Крутизна склонов варьирует от 25° до 45°. Длина береговой полосы составляет около 15.8 км, при этом одна третья часть ее приходится на валунно-галечниковые пляжи и две трети береговой полосы представлено скалистыми берегами и мысами. Летняя температура воздуха на острове Матыкиль варьирует от +7°C до +12°C. Годовая сумма осадков около 500 мм. Часто Ямские острова бывают укрыты туманом. Не менее девяти месяцев в году акватория Ямского архипелага покрыта дрейфующими льдами; море очищается ото льда в конце мая – середине июня. Летом штилевая погода держится недолго. Для района характерны частые перепады давления, быстрая смена погоды и внезапные шторма (скорость ветра во время шторма 25–35 м/с). Проливы между островами и районы вблизи мысов характеризуются сильными приливно-отливными течениями. Амплитуда приливов достигает 5–6 м, скорость течений – 13–17 км/ч. Высадка на остров Матыкиль возможна только на северной стороне острова в бухте Лагерной, которая защищена от северных и северо-восточных ветров скалистым мысом (Андреев, 2011).

Район Ямских островов является одним из высокопродуктивных по фитопланктону участков Охотского моря, а залив Шелихова считается одной из самых продуктивных акваторий Мирового океана (Шунтов, 1985). Через акваторию архипелага в залив Шелихова мигрируют представители рода *Oncorhynchus* Suckley, 1861, *Clupea pallasii* Valenciennes, 1847, *Mallotus villosus* Müller, 1776. Склоны острова Матыкиль покрыты травянистой растительностью. На острове Матыкиль гнездится 12 видов морских птиц, общая численность которых оценивается в 4 770 000 особей (Зеленская, 2009). Из млекопитающих здесь обитают *Clethorionomys rutilus* Pallas, 1779, несколько пар *Vulpes vulpes* Linnaeus, 1758. На южной стороне острова Матыкиль имеется небольшая залежка *Erignathus barbatus* Erxleben,

1777. С восточной стороны острова Матыкиль располагаются три лежбища сивуча, отделенные друг от друга небольшими выступающими в море мысами-непропусками. По центру располагается репродуктивное лежбище, расположенное на полосе галечного пляжа, протяженностью около 300 м и шириной 30–60 м. Со стороны берега лежбище ограничено крутым склоном. К северу и к югу от него находятся холостяковые залежки, где располагаются молодые животные (возраст: 1–3 года) и взрослые самцы.

Материалом для статьи послужили фотографии, полученные в период с 2013 по 2021 гг. с помощью шести автономных автоматических архивных регистраторов, установленных на склоне над репродуктивным лежбищем сивуча на острове Матыкиль. Автономные автоматические фоторегистраторы были специально сконструированы и изготовлены сотрудниками Камчатского филиала Тихоокеанского института географии ДВО РАН. Каждый фоторегистратор был полностью автономным. Он состоял из модифицированного герметичного бокса «Pelican», фотоаппарата с матрицей высокого разрешения (Canon EOS 1100D, 12.2 МП – 12.6 МП), объектива Canon EF-S 18–135 mm, f/3.5–5.6, портативного аккумулятора, солнечной батареи и блока управления системой (таймер, сумеречный выключатель и др.), который включал систему с наступлением рассвета, фотографировал участок лежбища, на который была направлена фотокамера, через запрограммированные интервалы времени, и выключал систему с наступлением темноты (рис. 2A,B). Фотографии записывались и сохранялись на карте памяти объемом 128 Гб.

Чтобы получить фотографии, необходимо было посетить остров Матыкиль и вручную заменить карты памяти в каждой камере. С 2013 по 2018 гг. обслуживание камер производилось один раз в год, в середине лета. В 2019 и 2020 гг. из-за логистических и финансовых трудностей посетить остров не представилось возможным, и камеры проработали в автономном режиме три года подряд до августа 2021 г. Фоторегистраторы были прикручены анкер-болтами в углублениях скал или рельефа крутого склона над лежбищем на всем его протяжении таким образом, чтобы падающие сверху камни и сход снежных лавин их не повредили. Каждая камера снимала только определенный участок лежбища с небольшим перекрытием от соседних камер. Таким образом, просматривая фотографии за одно и то же время (оно было синхронизировано на всех камерах), мы получали панорамную фотографию почти всего репродуктивного лежбища. Интервал съемки устанавливался специальным переключателем во время обслуживания камеры. Камеры вели съемку с интервалом в 5–30 мин. Всего за восемь лет наблюдений фоторегистраторы находились на лежбище 2945 дней. От 53% до 89% (в среднем 72%) этого времени камеры снимали лежбище и животных. В зависимости от продолжительности светового дня каждая камера ежедневно делала от 15 до 130 снимков, в среднем 70 фотографий в сутки (рис. 2C,D). Всего за этот период было получено 721 927 снимков со всех регистраторов.

Отмечались случаи отказа в работе камер. Их причины, главным образом, были связаны с разрядкой батарей из-за недостатка солнечной энергии в зимний период (декабрь – февраль), когда дни были короткими и на солнечные панели намерзал снег и лед. Эффективность работы панелей в такие дни резко снижалась. Весной с увеличением светового дня, таянием снега и льда на поверхности солнечных панелей их производительность восстанавливалась, аккумуляторы снова заряжались и камеры продолжали работу без вмешательства человека.

Изредка отмечались технические отказы из-за нарушения герметичности пластикового бокса и попадания в него атмосферной влаги. Она вызывала коррозию проводов и контактов, а также запотевание стекла бокса, которое значительно ухудшало качество фотографий. В середине октября 2017 г. на камеру №5 со скалы упал крупный камень, который разбил защитный бокс «Pelican», и камера перестала работать. Заменить бокс удалось только летом 2021 г. Во время обслуживания камер в августе 2018 г. из-за ошибки оператора камера №3 оказалась выключена и не работала до следующего посещения острова Матыкиль в 2021 г. (табл. 1).

Просмотр и обработка фотографий производилась в ручном режиме в специально разработанной базе данных PhotoCount v2. Для подсчета численности каждое животное на фотографиях отмечалось маркером с указанием половозрастной группы (рис. 3A). При обнаружении на снимке меченых сивучей так же обозначали маркером с указанием ID животного, и вносили информацию о встречах (рис. 3B).

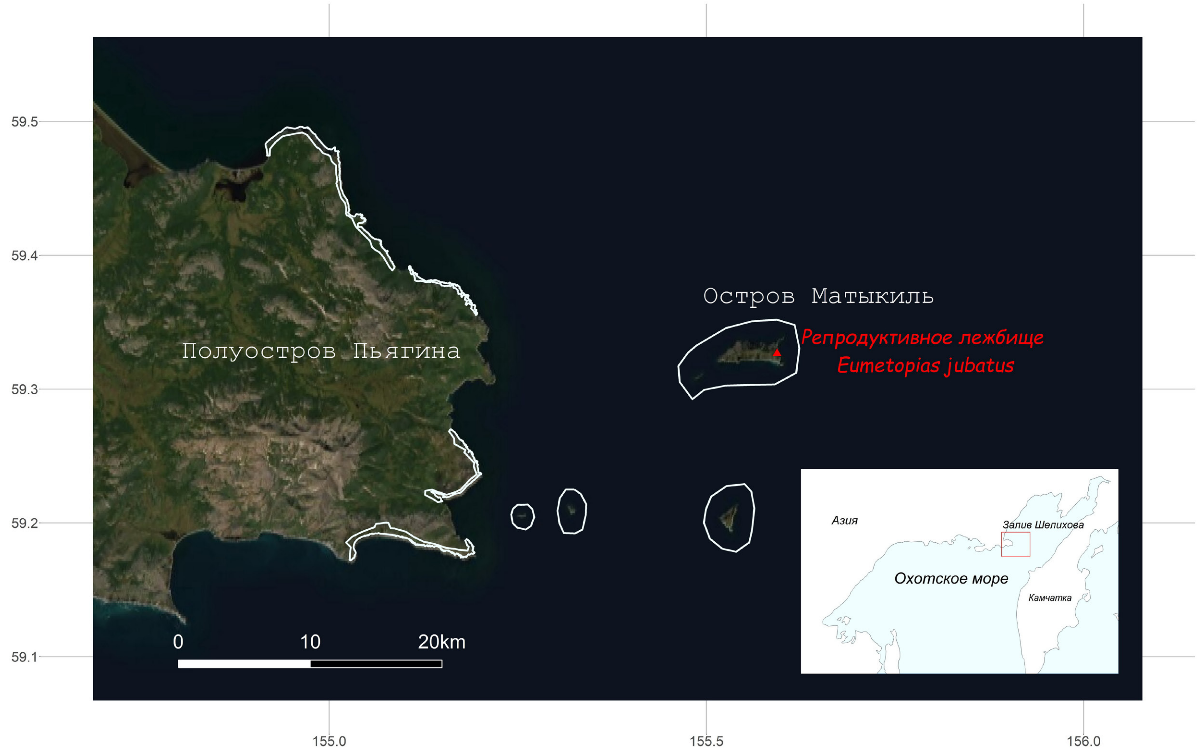

Рис. 1. Местоположение репродуктивного лежбища сивуча (*Eumetopias jubatus*) на острове Матыкиль. Белой линией обозначены границы Ямского участка (полуостров Пьягина и Ямские острова) заповедника «Магаданский» (Россия).
Fig. 1. The location of the Steller sea lion (*Eumetopias jubatus*) rookery on Matykil Island. The white line indicates the boundaries of the Yamsky section (Piagin Island and Yamsky Island) of the Magadan State Nature Reserve (Russia).

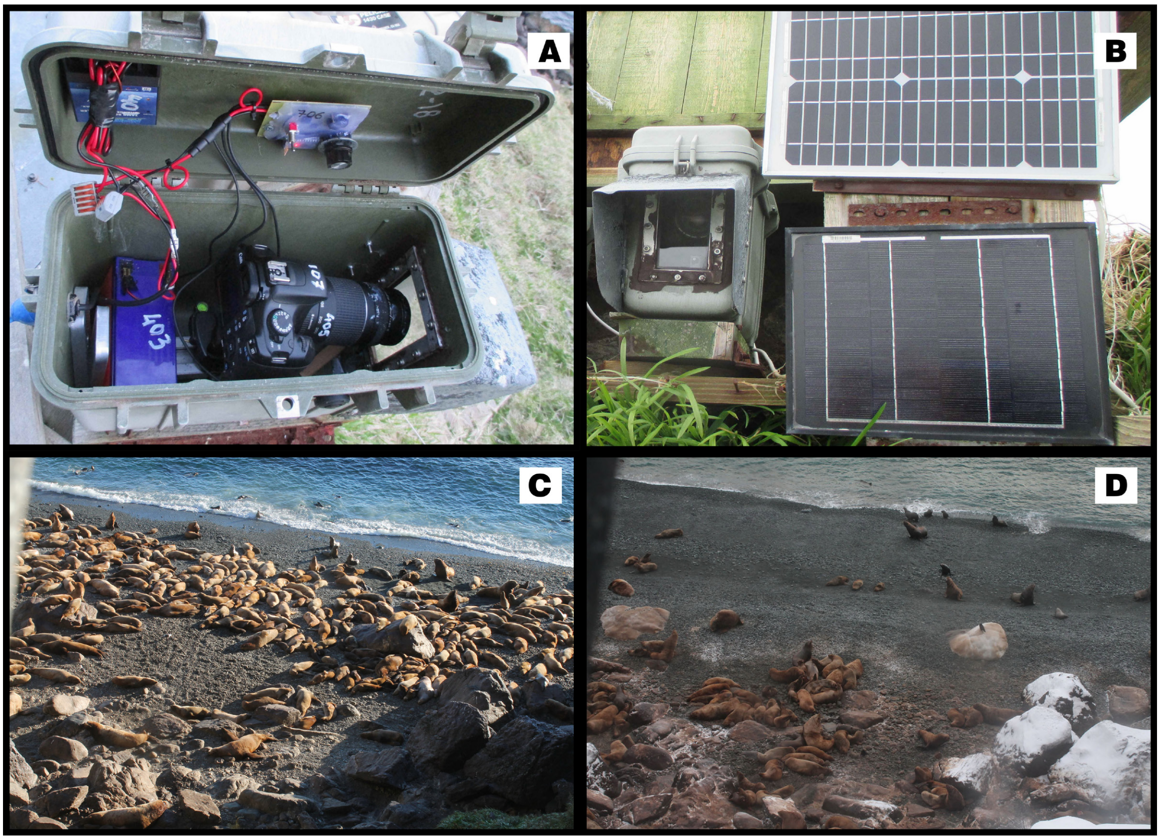

Рис. 2. Устройство и внешний вид автономных фоторегистраторов использованных на репродуктивном лежбище сивуча (*Eumetopias jubatus*) на острове Матыкиль (A, B) и пример фотографий полученных в разное время года: C – 22 августа, D – 1 декабря.
Fig. 2. Inside and outside views of autonomous automated archival remote time-lapse cameras used on Steller sea lion (*Eumetopias jubatus*) rookery (A, B) on Matykil Island, and examples of images collected at various time of the year: C – 22 August, D – 1 December.

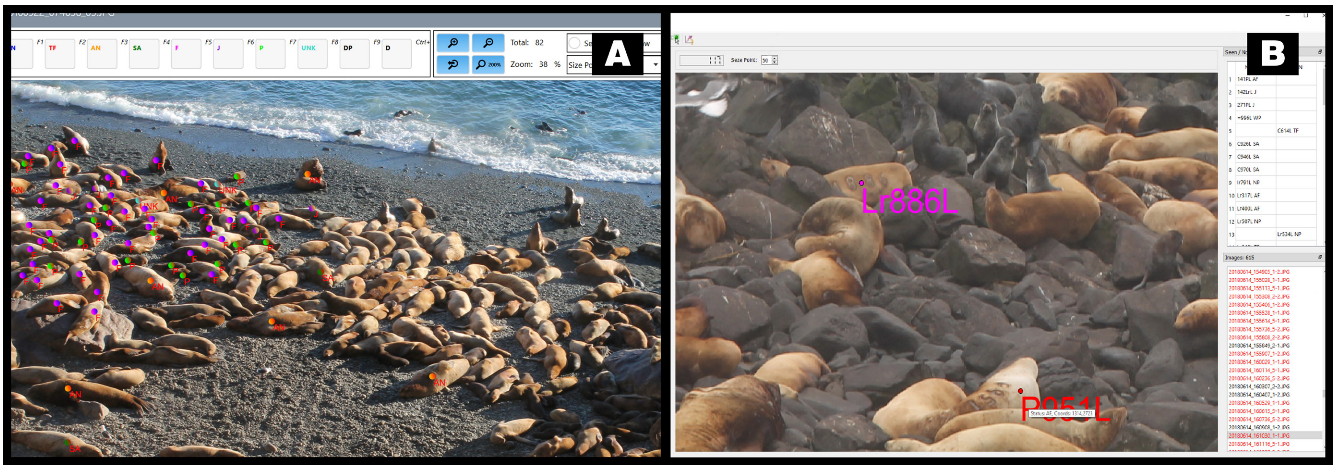

Рис. 3. Пример работы в модуле подсчета численности животных (A) и в модуле поиска меченых животных (B) базы данных PhotoCount v2.

Fig. 3. An example of working in the Count module (A) and in the brand search and registration module (B) in the PhotoCount v2 database.

Таблица 1. Количественные данные о работе автономных фоторегистраторов на репродуктивном лежбище сивуча (*Eumetopias jubatus*) на острове Матыкиль, 2013–2021 гг.

Table 1. The number of working days of autonomous automated time-lapse cameras at the Steller sea lion (*Eumetopias jubatus*) rookery on Matykil Island in 2013–2021

Год	Дней на лежбище	Количество дней, когда камера снимала лежбище					
		Камера 1	Камера 2	Камера 3	Камера 4	Камера 5	Камера 6
2013	166	141	151	165	54	166	166
2014	365	242	253	278	138	321	365
2015	365	263	263	312	315	263	360
2016	366	365	366	366	340	237	243
2017	365	365	347	338	306	210	113
2018	365	363	285	153	301	0	253
2019	365	363	45	0	317	0	70
2020	366	366	0	0	308	0	0
2021	223	163	0	11	198	0	0
Всего	2945	2631	1710	1623	2277	1197	1570
%	100%	89%	58%	55%	77%	74%*	53%

Примечание: * – до 2018 г., пока камера находилась в рабочем состоянии.

Для слежения за сезонной численностью животных на лежбище и характером использования его сивучами на протяжении годового цикла жизни было достаточно подсчитать животных на одной фотографии в день с каждой камеры. Для этого мы брали один качественный снимок с каждой камеры, снятый в период с 12:00 ч. до 14:00 ч. Количество сивучей на всех снимках, сделанных в одно и то же время дня, отражало лишь численность зверей на тех участках лежбища, на которые были направлены жестко зафиксированные объективы камер. На лежбище оставалось несколько небольших скрытых участков, на которых животные не были видны на снимках. Поэтому данные по численности, приводимые в нашей работе, объективно несколько занижены и не отражают общую численность животных на репродуктивном лежбище острова Матыкиль. Но эти данные позволяют проследить характер сезонного использования сивучами этого лежбища и получить детальное представление о половом и возрастном составе животных в течение всего года. На других лежбищах сивуча на острове Матыкиль камеры отсутствовали. Поэтому наши данные не отражают общую численность сивуча на этой территории.

Для поиска и идентификации меченых животных мы внимательно просматривали одну фотографию за каждый час съемки (т.е. брали лишь один из 2–12 снимков за час съемки, имеющихся в архиве). Обнаружив меченое животное, мы сравнивали его тавро с электронным каталогом меченых сивучей, записывали его пол, возраст и репродуктивный статус. Для настоящей работы мы использовали 60 632 фотографий (8.4% от общего числа полученных фотографий) и, главным образом, за период 2013–2017 гг.

В настоящее время для оценки численности и поиска тавреных сивучей мы начали разрабатывать компьютерный алгоритм, который значительно сокращает затраты времени на работу по извлечению информации из фотографий и в ближайшем будущем позволит нам использовать для анализа все данные по численности и меченым сивучам всего архива фотографий (Altukhov et al., 2021). Таким образом, в данной работе приводятся результаты анализа небольшой части архива.

Результаты

Массовый подход животных на лежбище начинается в середине апреля и продолжается до начала июля (максимальная численность: 1003–1073 особей), после чего число сивучей на лежбище снижается (табл. 2). Со второй половины августа количество тюленей начинает снова расти и достигает нового максимума в сентябре – начале октября (1159–1479 особей). В зимний период на репродуктивном лежбище находятся небольшие группы (до 80 особей) или одиночные сивучи. Возможно, их значительно больше выходит на другие нерепродуктивные лежбища острова, на которых камеры отсутствуют. В это время ежедневная численность на лежбище очень динамична и может изменяться в широких пределах (рис. 4, табл. П1).

Половозрастной состав животных, залегающих на берегу, непостоянен в течение года. Самки присутствуют на лежбище с мая по декабрь. Их максимальная численность приходится на первую декаду июля (табл. 2). Молодые животные (возрастом 1–3 года) встречаются на протяжении всего года за исключением февраля и марта. Их максимальная численность отмечается во второй – третей декаде сентября. Взрослые самцы (возрастом 8+ лет) и полусекачи (возрастом 4–7 лет) также присутствуют на лежбище в течение всего года, за исключением февраля и марта. Максимальная численность полусекачей приходится на конец августа – начало ноября, а взрослых самцов – на июнь (табл. 2). Таким образом, лежбище острова Матыкиль можно отнести к разряду смешанных. В любой сезон года на нем могут быть как самцы, так и самки любого возраста. В летний максимум численности на лежбище преобладали самки, однако в осенний максимум количество сивучей растет за счет подхода кочующих в поисках пищи молодых животных (возрастом 1–3 года) и полусекачей (самцы 4–7 лет).

Панорамные фотографии с фоторегистраторов не позволяли получать достоверные данные о численности новорожденных щенков, т.к. значительная часть лежбища покрыта крупными валунами и обломками скал, за которыми многие детеныши не видны. Так, если по данным с фоторегистраторов в период 2013–2017 гг. численность щенков на лежбище в среднем составляла 329 ± 25 (min–max: 293–369) особей, то во время прямого подсчета на лежбище в 2013 г. было учтено 477, а в 2017 г. – 620 живых щенков, т.е. на 23–53% больше.

Таблица 2. Средние показатели численности сивуча (*Eumetopias jubatus*) по половозрастным группам на репродуктивном лежбище острова Матыкиль по месяцам в 2013–2017 гг.

Table 2. The average number of Steller sea lion (*Eumetopias jubatus*) individuals of various age and sex groups on the Matykil Island’s rookery each month, 2013–2017

Месяц	Самки M ± 2SE (min–max)	Молодые особи M ± 2SE (min–max)	Полусекачи M ± 2SE (min–max)	Взрослые самцы M ± 2SE (min–max)
1	0.9 ± 2.1 (0–9)	1.7 ± 3.0 (0–13)	1.3 ± 2.0 (0–8)	1.7 ± 2.3 (0–8)
2	0.2 ± 0.4 (0–1)	0.5 ± 0.8 (0–3)	0.1 ± 0.3 (0–1)	0.1 ± 0.3 (0–1)
3	0.0	0.0 ± 0.2 (0–1)	0.0 ± 0.2 (0–1)	0.0 ± 0.2 (0–1)
4	0.2 ± 0.7 (0–3)	2.1 ± 7.2 (0–50)	8.0 ± 16.6 (0–79)	6.1 ± 11.9 (0–48)
5	69.3 ± 68.9 (0–225)	32.4 ± 26.1 (0–114)	16.9 ± 11.0 (0–44)	42.5 ± 16.0 (6–78)
6	320.7 ± 96.4 (34–545)	51.8 ± 26.5 (1–119)	8.0 ± 4.5 (0–21)	64.8 ± 11.9 (36–90)
7	415.3 ± 84.3 (105–613)	95.4 ± 33.5 (9–190)	7.4 ± 3.6 (0–19)	55.7 ± 11.7 (18–76)
8	229.1 ± 76.9 (82–425)	83.0 ± 38.6 (7–172)	20.0 ± 18.0 (1–85)	32.5 ± 13.2 (6–65)
9	353.1 ± 95.6 (1–523)	157.9 ± 47.3 (6–266)	45.8 ± 24.7 (1–120)	47.9 ± 18.7 (0–84)
10	282.2 ± 128.0 (58–643)	115.1 ± 53.1 (21–266)	42.9 ± 22.4 (5–94)	41.2 ± 19.3 (7–92)
11	117.6 ± 72.7 (13–297)	59.5 ± 33.7 (6–157)	31.4 ± 18.7 (1–89)	31.7 ± 11.9 (10–55)
12	34.5 ± 38.2 (0–165)	18.6 ± 19.5 (0–79)	9.3 ± 9.2 (0–37)	14.9 ± 10.5 (0–37)

Примечание: M – среднее арифметическое, 2SE – 95% доверительный интервал, min – минимальное значение, max – максимальное значение.

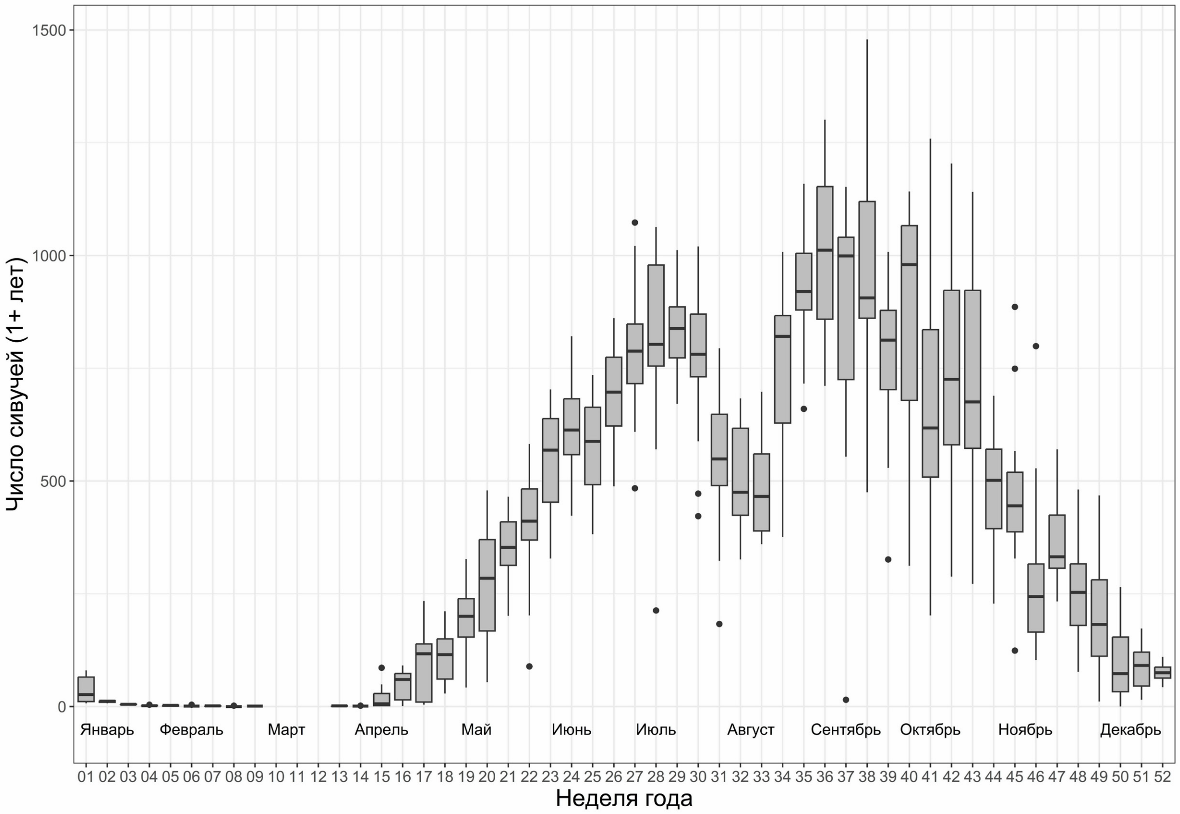

Рис. 4. Сезонная динамика численности сивуча (*Eumetopias jubatus*) на репродуктивном лежбище острова Матыкиль в 2013–2017 гг. Верхние и нижние границы прямоугольников обозначают первый и третий квартили; вертикальные линии («усы») – интервалы, в которые попадает подавляющее большинство наблюдений, не превышающих значения 1.5 межквартильного размаха; горизонтальная линия обозначает медиану; точки обозначают выбросы значений.
Fig. 4. The seasonal abundance of Steller sea lion (*Eumetopias jubatus*) individuals on the Matykil Island's rookery in 2013–2017. The upper and lower borders of the boxes denote the first and third quartiles; vertical lines («whiskers») denote the intervals, in which the vast majority of observations fall, not exceeding the value of 1.5 interquartile range of values; the horizontal line denotes the median; dots denote outliers.

В 2013–2017 гг. на снимках с фоторегистраторов на лежбище всего было обнаружено 276 тавреных сивучей. В среднем в период 2013–2016 гг. регистрировалось 154 ± 2.2 (min–max: 116–182) меченых животных в год. В 2017 г. было зарегистрировано 96 тавреных сивучей, что связано с небольшим объемом просмотренных фотографий, ограниченных репродуктивным периодом. Среди них преобладали животные местного происхождения. В репродуктивный период они составляют 82.7% от общего числа обнаруженных на лежбище тавреных сивучей, а в осенний период – 68.9%. Сивучи-мигранты, посетившие лежбище острова Матыкиль, по своему происхождению были представлены животными почти со всех лежбищ Дальнего Востока России за исключением животных с Командорских островов. Всего в 2013–2017 гг. было зарегистрировано 131 животное неместного происхождения. Наиболее часто встречались сивучи с островов Тюлений (36.6%), Ионы (16.0%), Каменные Ловушки (13.7%), реже с острова Брат Чирпоев (6.8%), островов Среднего (6.1%), Райкоке (9.9%), Анциферова (9.9%) и мыса Козлова у Восточной Камчатки (0.7%). Среди меченых мигрантов, в основном, были молодые сивучи и полусекачи. Большинство сивучей-мигрантов (61.8%) наблюдались на острове Матыкиль лишь один сезон. Некоторые посещали лежбище два года и больше (табл. 3). Но, как правило, при достижении репродуктивного возраста они покидали остров Матыкиль. За период исследований было зарегистрировано шесть самок-мигрантов репродуктивного возраста (4 + лет), а две из них отмечены на лежбище с новорожденными щенками. Взрослые самцы (8 + лет) с других лежбищ в репродуктивный период не встречались.

В 2015 г. в поле зрения камер фоторегистраторов попал молодой самец *Zalophus californianus* Lesson, 1828. Он отмечался на лежбище два дня, 7 и 8 сентября.

Таблица 3. Число повторных встреч сивучей-мигрантов на острове Матыкиль в 2013–2017 гг.
Table 3. The number of repeat sightings of migrant Steller sea lions (*Eumetopias jubatus*) on the Matykil Island's rookery in 2013–2017

Год	Число повторно встреченных животных в разные годы				
	2013	2014	2015	2016	2017
2013	69 (100%)	26 (37.7%)	12 (17.4%)	3 (4.3%)	1 (1.4%)
2014	–	49 (100%)	22 (44.9%)	5 (10.2%)	1 (2.0%)
2015	–	–	54 (100%)	7 (13.0%)	1 (1.9%)
2016	–	–	–	12 (100%)	4 (33.3%)
2017	–	–	–	–	19 (100%)

Примечание: в скобках указана доля повторно встреченных животных в последующие года после первой их регистрации.

Обсуждение

До момента установки автономных регистраторов и начала круглогодичного мониторинга сивуча на острове Матыкиль считалось, что сивучи подходят к лежбищу в начале мая и держатся там до конца сентября – начала октября, а в зимний период животные отсутствуют на лежбище (Андреев, 2011). Однако мы обнаружили, что в настоящий момент массовый подход сивучей начинается раньше, с середины апреля, и животные находятся на лежбище вплоть до конца декабря. В зимние месяцы на берегу остаются небольшие группы сивучей. Исключением является март, когда вокруг острова Матыкиль образуются плотные и обширные ледовые поля, препятствующие выходу животных на берег. Мы полагаем, что в это время сивучи для отдыха используют лед и при появлении первых разводий тут же возвращаются на остров Матыкиль. Таким образом, сивучи обитают в районе Ямских островов круглый год. В течение года отмечается два пика численности: летний, который происходит в результате подхода сивучей к лежбищу для размножения, и осенний – вследствие миграции животных с других лежбищ.

Представленные в работе данные по общей численности молодых и взрослых сивучей на острове Матыкиль занижены по двум причинам. Во-первых, фоторегистраторы установлены только на репродуктивном лежбище, и две холостяковые залежки остаются вне поля зрения объективов камер. Во-вторых, численность животных на фотографиях с фоторегистраторов, как правило, оказывается заниженной (Marcotte, 2006; Goto et al., 2022). Это связано с особенностями установки камер, характером залегания сивучей (чем плотнее залежка, тем больше ошибка подсчета зверей). К сожалению, нам не удалось сравнить данные численности с фоторегистраторов и данные аэрофотосъемки с беспилотного летательного аппарата (БПЛА) из-за технических проблем (не работала одна из наземных камер в момент аэросъемки или же в ходе посещения лежбища часть животных сходила в воду и в дальнейшем переходила на соседние залежки).

По данным исследователей предыдущих лет, в репродуктивный период доля сивучей местного происхождения составляла 84.5–86.0%. Сивучи-мигранты были, в основном, представлены молодыми самцами, а доля половозрелых самок составляла не более 6% (Грачев, Бурканов, 2005, 2015). Наши данные также подтверждают эти сведения.

Заключение

В целом, несмотря на отдельные технические сбои в работе, автоматические автономные фоторегистраторы позволяют эффективно вести многолетний круглогодичный мониторинг сивучей на удаленном лежбище острова Матыкиль и получать достоверную информацию о присутствии и размножении меченых (тавреных) животных. Для точной оценки общей численности сивучей на изучаемом репродуктивном лежбище необходимо обследование и подсчет животных на всех лежбищах одновременно. Обустройство нерепродуктивных лежбищ дополнительными камерами и серия параллельных учетов по изображениям с фиксированных камер и аэрофотоучетов с БПЛА позволят определить погрешность оценки общей численности с помощью фиксированных камер и дадут возможность более точно и полно проследить динамику общей численности сивуча на всем острове Мытыкиль. Несмотря на недооценку общей численности, на основании полученных данных можно сделать надежные выводы, что сезонная численность сивучей на протяжении 2013–2017 гг. на острове Матыкиль закономерно изменялась в широких пределах, но без явно выраженного межгодового тренда. В настоящее время применение автономных фоторегистраторов является единственным доступным методом круглогодичного мониторинга лежбищ сивуча в удаленных и труднодоступных районах, подобных лежбищу на острове Матыкиль.

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Дополнительная информация

Дополнительная информация к статье Кирилловой и др. (2024) может быть найдена в **Электронном приложении**.

Литература

Алтухов А.В., Бурканов В.Н., Рязанов С.Д. 2011. Автономная фотосистема для мониторинга лежбищ сивучей // Дистанционные методы исследования в зоологии. М.: Товарищество научных изданий КМК. С. 4.

Андреев А.В. 2011. Природные условия участков заповедника // Растительный и животный мир заповедника «Магаданский». Магадан: СВНЦ ДВО РАН. С. 6–46.

Бурканов В.Н., Алтухов А.В., Желетт Т.С. 2015. Использование автономных фоторегистраторов для мониторинга лежбищ сивуча (*Eumetopias jubatus*) в России и на Аляске // Морские млекопитающие Голарктики. Т. 1. Москва. С. 106.

Грачев А.Н., Бурканов В.Н. 2005. Предварительные результаты исследований сивуча на репродуктивном лежбище о. Матыкиль в 2005 г. // Сохранение биоразнообразия Камчатки и прилегающих территорий. Петропавловск-Камчатский: Камчатпресс. С. 236–239.

Грачев А.Н., Бурканов В.Н. 2015. Мониторинг состояния лежбища сивучей на о. Матыкиль (Ямский участок заповедника) // Научные исследования редких видов растений и животных в заповедниках и национальных парках Российской Федерации за 2005–2014 гг. Вып. 4. М.: ВНИИ Экология. С. 178–180.

Задальский С.В. 2000. Состояние популяции и миграции сивучей в северной части Охотского моря // Морские млекопитающие Голарктики. Архангельск. С. 123–125.

Зеленская Л.А. 2009. Численность и распределение морских птиц на острове Матыкиль (Ямские острова, Охотское море) // Зоологический журнал. Т. 88(5). С. 546–555.

Красная книга Российской Федерации. Том Животные. Издание 2-е. М.: ВНИИ Экология, 2021. 1128 с.

Шунтов В.П. 1985. Биологические ресурсы Охотского моря. М.: Агропромиздат. 224 с.

Altukhov A., Andrews R., Burkanov V., Usatov I., Gelatt T. 2021. Improving the Performance of Convolutional Neural Network (CNN) Algorithms for Automated Image Recognition of Branded Steller Sea Lions // 2021 Alaska Marine Science Symposium. Anchorage, Alaska, USA. P. 146.

Boveng P.L., London J.M., Badajos O. 2011. Distribution and abundance of harbor seals in Cook Inlet, Alaska. Task II: Assessment of Factors Influencing Harbor Seal Haul-out Behavior Using Remote Time-Lapse Cameras, 2003–2005. Final Report. BOEM Report 2011-064. Anchorage: Bureau of Ocean Energy Management. 50 p.

Burkanov V.N., Loughlin T.R. 2005. Distribution and Abundance of Steller Sea Lions, *Eumetopias jubatus*, on the Asian Coast, 1720's–2005 // Marine Fisheries Review. Vol. 67(2). P. 1–62.

Goto Y., Isono T., Ikuta S., Burkanov V. 2022. Origin and Abundance of Steller Sea Lions (Eumetopias jubatus) in Winter Haulout at Benten-Jima Rock Off Cape Soya, Hokkaido, Japan between 2012–2017 // Mammal Study. Vol. 47(2). P. 87–101. DOI: 10.3106/ms2020-0029

Holt R.D. 2019. Pacific walrus terrestrial haul-out use on Togiak National Wildlife Refuge, Alaska, 1985–2018. Dillingham, Alaska: U.S. Fish and Wildlife Service; Togiak National Wildlife Refuge. 45 p.

Kulinchenko A.B., Rogers E.O., Kopylova Y., Olsen E., Andrews J., Simpson P.K., Jones M. 2004. Steller Watch time-lapse photography system for remote Steller Sea Lion sites // 2004 IEEE International Geoscience and Remote Sensing Symposium. Vol. 2. Anchorage, Alaska, USA. P. 1447–1450. DOI: 10.1109/IGARSS.2004.1368692

Loughlin T.R., Perlov A.S., Vladimirov V.A. 1992. Range-wide survey and estimation of total number of Steller sea lions in 1989 // Marine Mammal Science. Vol. 8(3). P. 220–239. DOI: 10.1111/j.1748-7692.1992.tb00406.x

Marcotte M. 2006. Steller Watch: timing of weaning and seasonal patterns in numbers and activities of Steller sea lions at a year-round haulout site in Southeast Alaska. MSc. Thesis. Vancouver: University of British Columbia. 82 p.

References

Altukhov A.V., Burkanov V.N., Ryazanov S.D. 2011. Automated photo system for Steller sea lion rookeries surveillance. In: V.V. Rozhnov (Ed.): *Remote Methods of Research in Zoology*. Moscow: KMK Scientific Press Ltd. P. 4. [In Russian]

Altukhov A., Andrews R., Burkanov V., Usatov I., Gelatt T. 2021. Improving the Performance of Convolutional Neural Network (CNN) Algorithms for Automated Image Recognition of Branded Steller Sea Lions. In: *2021 Alaska Marine Science Symposium*. Anchorage, Alaska, USA. P. 146.

Andreev A.V. 2011. Natural conditions of the state nature reserve's sites. In: *Flora and fauna of the Magadan State Nature Reserve*. Magadan: North-East Scientific Center FEB RAS. P. 6–46. [In Russian]

Boveng P.L., London J.M., Badajos O. 2011. *Distribution and abundance of harbor seals in Cook Inlet, Alaska. Task II: Assessment of Factors Influencing Harbor Seal Haul-out Behavior Using Remote Time-Lapse Cameras, 2003–2005*. Final Report. BOEM Report 2011-064. Anchorage: Bureau of Ocean Energy Management. 50 p.

Burkanov V.N., Loughlin T.R. 2005. Distribution and Abundance of Steller Sea Lions, Eumetopias jubatus, on the Asian Coast, 1720's–2005. *Marine Fisheries Review* 67(2): 1–62.

Burkanov V.N., Altukhov A.V., Gelatt T.S. 2014. Monitoring of the Steller sea lion (*Eumetopias jubatus*) rookeries with the time-lapse cameras in Russia and Alaska. In: *Marine Mammals of the Holarctic*. Vol. 1. Moscow. P. 106. [In Russian]

Goto Y., Isono T., Ikuta S., Burkanov V. 2022. Origin and Abundance of Steller Sea Lions (*Eumetopias jubatus*) in Winter Haulout at Benten-Jima Rock Off Cape Soya, Hokkaido, Japan between 2012–2017. *Mammal Study* 47(2): 87–101. DOI: 10.3106/ms2020-0029

Grachev A.I., Burkanov V.N. 2005. The preliminary results of Steller sea lion investigations on the rookery of Matykil' Island (Yamsky Islands) in 2005. In: R.S. Moiseev, A.M. Tokranov, O.A. Chernyagina (Eds.): *Conservation of the biodiversity of Kamchatka and adjacent seas*. Petropavlovsk-Kamchatsky: Kamchatpress. P. 236–239. [In Russian]

Grachev A.I., Burkanov V.N. 2015. Monitoring of the Steller sea lion rookery on Matykil' Island (Yamsky section of the state nature reserve). In: D.M. Ochagov, R.I. Nazyrova, N.A. Potapova, N.A.Vilyaeva (Eds.): *Scientific studies of rare species of plants and animals in strict nature reserves and national parks of the Russian Federation for the period of 2005–2014*. Vol. 4. Moscow: VNII Ecologiya. P. 178–180. [In Russian]

Holt R.D. 2019. *Pacific walrus terrestrial haul-out use on Togiak National Wildlife Refuge, Alaska, 1985–2018*. Dillingham, Alaska: U.S. Fish and Wildlife Service; Togiak National Wildlife Refuge. 45 p.

Kulinchenko A.B., Rogers E.O., Kopylova Y., Olsen E., Andrews J., Simpson P.K., Jones M. 2004. Steller Watch time-lapse photography system for remote Steller Sea Lion sites. In: *2004 IEEE International Geoscience and Remote Sensing Symposium*. Vol. 2. Anchorage, Alaska, USA. P. 1447–1450. DOI: 10.1109/IGARSS.2004.1368692

Loughlin T.R., Perlov A.S., Vladimirov V.A. 1992. Range-wide survey and estimation of total number of Steller sea lions in 1989. *Marine Mammal Science* 8(3): 220–239. DOI: 10.1111/j.1748-7692.1992.tb00406.x

Marcotte M. 2006. *Steller Watch: timing of weaning and seasonal patterns in numbers and activities of Steller sea lions at a year-round haulout site in Southeast Alaska*. MSc. Thesis. Vancouver: University of British Columbia. 82 p.

Red Data Book of the Russian Federation. Animals. 2nd ed. Moscow: VNII Ecologiya, 2021. 1128 p. [In Russian]

Shuntov V.P. 1985. *Biological resources of the Sea of Okhotsk*. Moscow: Agropromizdat. 224 p. [In Russian]

Zadalsky S.V. 2000. Population status and migration of Steller sea lions in the northern part of the Sea of Okhotsk. In: *Marine Mammals of the Holarctic*. Arkhangelsk. P. 123–125. [In Russian]

Zelenskaya L.A. 2009. The number and distribution of birds on Matykil Island (the Yamskie Islands, the Sea of Okhotsk). *Zoologicheskii Zhurnal* 88(5): 546–555. [In Russian]

LONG-TERM REMOTE MONITORING OF THE ROOKERY OF *EUMETOPIAS JUBATUS* (PINNIPEDIA, OTARIIDAE) ON MATYKIL ISLAND IN THE MAGADAN STATE NATURE RESERVE (RUSSIA)

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The severe decline in the number of *Eumetopias jubatus* (hereinafter – Steller sea lion) almost throughout the entire range has drawn the public attention to monitor the abundance and increase in research activity of the species. In Russia, such a study has been conducted regularly since the early 2000s. It includes range-wide population surveys in the Russian Far East, marking newborn pups and monitoring their survival, movements, and reproduction success. In the first decade of the XXI century, observers conducted direct observations on rookeries during the breeding season. Since 2011 a novel survey method has been used, using custom-made autonomous high-resolution remote cameras, which have been taking images of the rookeries all year round. In 2013, six remote-camera units were installed in the Magadan State Nature Reserve (Russia) at the rookery of the Steller sea lion located on Matykil Island. The cameras gathered images during day time every 5–30 min. Maintenance of the photo recorders was carried out once per year in the summer period. A total of 721 927 photographs were collected during eight years of the surveys. Of them, 60 632 photographs were manually analysed in this research. It was found that the Steller sea lions use the rookery throughout the year, with the exception of March when a dense and wide ice cover in the study area prevents the Steller sea lions from reaching the shore of Matykil Island. During the year, two peaks of the Steller sea lion population abundance were observed, namely summer and, with a higher number of individuals, in autumn. In summer, females predominate on the rookery, while in the autumn-winter period, young animals (mainly males) and mature (8+ years) adults. In winter, the number of Steller sea lions was low on the shore. We have seen branded Steller sea lions on Matykil Island from all rookeries in the Russian Far East, with the exception of animals born on the Commander Islands. The highest number of migrant Steller sea lions appears in the autumn period, and it is represented mainly by young animals (1–3 years old) and semi-adults (males aged 4–7 years). In general, the data obtained from images collected by remote cameras during the entire year provided a detailed picture of the rookery used by Steller sea lions during the entire annual cycle of their life and monitored the seasonal population dynamics, the sex and age composition of animals on the shore, and the reproductive success of marked Steller sea lions. Currently, the use of autonomous remote cameras remains the only available method of year-round monitoring of the state and habitat use of hard-to-reach remote Steller sea lion's rookeries.

Key words: abundance, age-sex composition, branding, counts, marking, remote camera, seasonal population dynamics, Steller sea lion, Yamskie Islands

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BEHAVIOURAL LATERALISATION OF SWANS IN RESPONSE TO ANTHROPOGENIC DISTURBANCE DIFFERS ACCORDING TO THE LOCOMOTION TYPE

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The European population of *Cygnus columbianus bewickii* has a declining trend in number of individuals. Anthropogenic disturbance could be one of the reasons for this decline. Disturbance influences animal behaviour, including the manifestation of behavioural lateralisation. Therefore, investigating the impact of anthropogenic disturbance on behavioural lateralisation is essential for biodiversity conservation. Behavioural lateralisation manifests itself in a preference to use one of two paired organs (limbs or sensory organs) and a preference to avoid obstacles from a certain side. Earlier studies of behavioural lateralisation did not consider the locomotion type as an independent variable factor in the analysis, although it could affect the manifestation of behavioural lateralisation. We studied the influence of anthropogenic disturbance on behavioural lateralisation of swans, depending on the type of locomotion (swimming or flying). We have analysed 492 photos from aerial counts of two swan species (*Cygnus columbianus bewickii*, *C. cygnus*) in Yamal Peninsula and Gydan Peninsula. The photos were taken from a plane, while the birds were escaping from it as a source of anthropogenic disturbance. Pairs without and with chicks alone or in flocks were encountered swimming or flying. We found that swimming swans had a strong right-sided bias and right-eye bias for avoidance and observing the source of anthropogenic disturbance, and flying swans had a left bias. Swimming *C. c. bewickii* and *C. cygnus* exhibited similar behavioural lateralisation. These results were the same for following and leading birds. The presence of chicks did not change the direction of behavioural lateralisation but strengthened it for the following partners. The differences in behavioural lateralisation could be caused by the fact that swans in flight experience greater fear of a present aircraft than when they are on water. We conclude that the locomotion types influence behavioural lateralisation in response to anthropogenic disturbance. We recommend paying attention to accompanying factors when comparing the results of lateralisation studies. As the left side bias of flying birds in our study indicates that flying birds are more stressed than swimming ones, we recommend not forcing birds to fly during observations to reduce their stress.

Key words: anxiety, chicks, *Cygnus columbianus bewickii*, *Cygnus cygnus*, flying, Gydan Peninsula, motor lateralisation, swimming, visual lateralisation, Yamal Peninsula

Introduction

Anthropogenic disturbance affects animal behaviour by increasing vigilant behaviour and decreasing feeding and resting behaviour (Riddington et al., 1996; Kruckenberg et al., 2008; Bellebaum & Kruckenberg, 2009). As a result, feeding intensity, accumulation of body reserves, chicks' survival, and breeding success are reduced (Black, 2001; Mainguy et al., 2002; Féret et al., 2005). The impact may be especially strong for threatened species with small or declining populations. However, changes in behaviour under anthropogenic disturbance manifest themselves not only in changes in the proportions of various types of behaviour. In our study, we focused on the impact of anthropogenic disturbance on behavioural lateralisation.

Lateralised processing by the nervous system is a property of most bilaterally symmetrical animals (Rogers et al., 2013). The dominance of one brain hemisphere in the implementation of any function can be manifested in animal behaviour in the form of one-sided preferences, such as a limb-use preference for various tasks (Friedmann & Davis, 1938; Vince, 1964; Davies & Green, 1991; Rogers & Workman, 1993; Gutiérrez & Soriano-Redondo, 2020), avoiding a collision with an obstacle from either side in flight (Bhagavatula et al., 2014), spinning in one direction while feeding on water (Gutiérrez & Soriano-Redondo, 2020), or inspecting a stimulus with one eye (Rogers et al., 2013). The lateralisation bias of the brain allows avoiding conflicts between various behaviours performed simultaneously and increases brain productivity and compactness (Levy, 1977; Vallortigara et al., 2011; Vallortigara & Versace, 2017; Vallortigara

& Rogers, 2020). Lateralised animals are more successful in such important survival tasks as feeding and avoiding predators (Güntürkün et al., 2000; Rogers et al., 2004). Furthermore, there is evidence that the degree of lateralisation is positively correlated with cognitive ability (Magat & Brown, 2009; Vallortigara & Rogers, 2020).

In the vertebrate animal brain, including the avian brain, the optic nerves cross virtually completely, and the input from the left eye is mostly confined to structures of the right hemisphere and vice versa (Workman & Andrew, 1986; Rashid & Andrew, 1989; Jeffery & Erskine, 2005). Previous studies demonstrated that a lateralisation bias for the left hemisphere and right eye appears in the processing of positively connoted emotions (Leliveld et al., 2013) and provides more subtle differences between food and non-food items (Mench & Andrew, 1986; Alonso, 1998; Güntürkün et al., 2000). A bias for the right hemisphere and left eye is common in novelty detection (Rogers & Kaplan, 2005; Charles et al., 2021) and responsible for negative emotions such as aggression (Vallortigara et al., 2001; Krakauer et al., 2016; Rogers et al., 2018) and fear (Dharmaretnam & Rogers, 2005).

Nevertheless, in one type of behaviour, animals may have opposite biases according to the circumstances. When animals see or hear actual predators or threats, the left-eye-right-hemisphere system is responsible for predator detection in birds (Rogers & Kaplan, 2005; Koboroff et al., 2008; Rogers et al., 2018), mammals (Austin & Rogers, 2014), and reptiles (Martín et al., 2010; Bonati et al., 2013). In anti-predator vigilance for potential (not actual) predators, animals prefer to use the right eye for scanning the environment (*Junco hyemalis* Linnaeus, 1758 (Franklin & Lima, 2001), *Anser cygnoides* Linnaeus, 1758, *Fulica atra* Linnaeus, 1758 (Randler, 2005), and *Calidris pusilla* Linnaeus, 1766 (Beauchamp, 2013)).

It is important to note that in the above mentioned studies, birds used different types of locomotion. For instance, *Gymnorhina tibicen* Latham, 1801, used the left eye for the detection of threats by jumping, pecking at the predator, circling, or viewing it in an alert posture (Koboroff et al., 2008). Similar results were obtained for *Taeniopygia guttata* Vieillot, 1817, sitting on a perch in an experimental cage, and in *Gallus gallus domesticus* Linnaeus, 1758, staying in the centre of an experimental circular arena (Rogers, 2002). The opposite results were obtained when birds were walking during feeding (Franklin & Lima, 2001; Beauchamp, 2013). At the same time, locomotion types have not been investigated as an independent factor in earlier lateralisation studies. However, even in locomotion-controlled experiments, different species may show opposite lateralisation. While walking during feeding, *Junco hyemalis* directed their right eye outward more often than would be expected by chance, and *Spizella arborea* Wilson, 1810 had non-significant tendency to favour the left eye in the same locomotion type (Franklin & Lima, 2001). This suggests that laterality may differ even in closely related species.

The distance to the source of anthropogenic disturbance affects the manifestation of visual lateralisation as well. *Anser albifrons* Scopoli, 1769, feeding closely to the road, preferred to keep the source of disturbance in the left visual field. In contrast, geese located at a greater distance from the disturbance source observed it with the right eye (Zaynagutdinova et al., 2020). Furthermore, anthropogenic disturbance affects the manifestation of visual lateralisation not only in vigilant behaviour but in other behaviour as well. For example, a study of *Branta leucopsis* Bechstein, 1803 and *Anser albifrons* found that disturbance could influence the manifestation of visual lateralisation in observing the partner while feeding. Visual lateralisation was manifested under calm conditions and was lacking under disturbing conditions (Zaynagutdinova et al., 2021).

Information on motor lateralisation during flying and swimming is insufficient and requires more detailed studies. Bhangavatula et al. (2014) demonstrated individual motor lateralisation in flying *Melopsittacus undulates* Shaw, 1805 to avoid obstacles, but there were no significant results in *Tachycineta bicolor* Vieillot, 1808 at a population level (Mandel et al., 2008). Three shorebird species (*Phalaropus fulicarius* Linnaeus, 1758, *Phalaropus lobatus* Linnaeus, 1758, and *Phalaropus tricolor* Vieillot, 1819) showed significant motor lateralisation while feeding on water (Gutiérrez & Soriano-Redondo, 2020). Furthermore, it has been suggested that motor lateralisation might be due to visual lateralisation (Bhagavatula et al., 2014; Baciadonna et al., 2022).

Waterfowl are very sensitive to anthropogenic disturbance during breeding and moulting periods. Birds are especially vulnerable to disturbance while they are flightless. For example, *Cygnus columbianus* (Ord, 1815) loses their flight ability during moulting, which starts in the second half of the brood rearing period (Earnst, 1992). When waterfowl are not able to fly in the moulting period, their behaviour could differ from other periods. As precocial birds (Nice, 1962), waterfowl move a lot with their broods (Boiko & Kampe-Persson, 2012), and parents have to pay attention to their brood and monitor the environment simultaneously. These behavioural factors may affect behavioural lateralisation in a similar way for various species. As understanding the influences of disturbance effects on animal behaviour is essential for biodiversity conservation, we aimed to study the influence of anthropogenic disturbance on behavioural lateralisation in swans under various circumstances. Since the type of locomotion as an independent factor for the manifestation of behavioural lateralisation had not been investigated before, our task was to compare behavioural lateralisation in swimming and flying birds. Another task was to evaluate the sustainability of behavioural bias for particular locomotion types under various conditions: for leading and following birds, for families with or without chicks, and for phylogenetically closely related species.

Waterfowl could be a good model for such studies as it is possible to observe their walking, swimming, and flying behaviour. *Cygnus columbianus bewickii* Ord, 1815 (Koblik & Redkin, 2004), was chosen as an object for the study. The European population of *C. c. bewickii* has been declining (Beekman et al., 2019) and is considered Vulnerable (BirdLife International, 2021; Red Data Book of the Russian Federation, 2021). The reasons for the decline are not clear yet (Beekman et al., 2019). Anthropogenic disturbance could be one of the causes. The other species chosen for the study was the closely related *Cygnus cygnus* Linnaeus, 1758.

Material and Methods

Material collection

Previous studies have shown that *Cygnus c. bewickii* and *C. cygnus* breed on the Yamal Peninsula and the Gydan Peninsula, Western Siberia, Russia (Syroechkovski, 2002; Fang et al., 2020). We analysed photos of swans taken during aerial surveys conducted on these peninsulas between 24 June and 03 October in 2015–2017 and 2019–2020. These periods correspond to the brood rearing, moulting, and autumn migration of swans (Pennycuick et al., 1996; Boiko & Wikelski, 2019; Vangeluwe et al., 2018). The surveys were carried out using a Sterkh-1 aircraft, flying on sub-meridional transects or perpendicular to the sea coast. The co-ordinates of the transects were provided by local Fish and Game Service. The flights were conducted at an altitude of 38 m a.s.l. at a speed of 80–100 km/h. Photos were taken from both sides of the aircraft at a distance of up to 200 m for every bird or flock observed, with a total count width of 400 m. Photos were taken from both sides of the aircraft with equal probability. To eliminate repeated photos of the same birds, we analysed only those taken at a distance higher than 1 km from each other. Swans were observed swimming on the water or flying in the air, and only the first photo of each pair of birds was included in the analysis. In total, we analysed 492 photos.

Analysis of the photos

We analysed 363 photos of pairs of *C. c. bewickii* and 129 photos of pairs of *C. cygnus*. *Cygnus c. bewickii* in the photos were swimming or flying. The swimming *C. c. bewickii* were with or without chicks. *Cygnus cygnus* were only observed swimming without chicks. We considered two swans a pair when there were only two swans in the photo and the distance between them was less than 10 m. If the birds were in a flock, we considered two swans a pair if they had a distance between each other of up to 3 m, and the other birds were more than 10 m away from them. The maximum flock size was 39 birds. The distance between swans was determined according to the size of the swan's body without its neck and head, which corresponds to 0.7 m. Consequently, we counted the number of bodies between the swans and multiplied this amount by 0.7. As a rule, one swan in a pair was behind the partner. In such cases, the first bird was classified as the leading bird, and the bird located behind was classified as the following bird. We also recorded the presence and absence of chicks in swan pairs. Birds could be moving in any direction relative to the plane. We determined the direction of escape and the side that the swans turned to the anthropogenic disturbance (aircraft). We included in the analysis only the photos with the swans turned to the aircraft on the right or left side. We supposed that swans use the right or left eye for observing the plane as the source of anthropogenic disturbance because the eyes of swans are positioned at the left and right side of the head. A study of another Anseriformes species, *Branta* *canadensis* Linnaeus, 1758, showed that the visual field for each eye is 135 degrees and the binocular overlap is 20 degrees (Heppner et al., 1985). Thus, the side vision is essential for geese and swans.

Statistical analysis

For our statistical analysis, we used samples of > 50 photos. The samples of *C. c. bewickii* without chicks included 65 leading flying birds and 65 following flying birds. We also included 103 leading swimming *C. c. bewickii* and 104 following swimming *C. c. bewickii* without chicks. The samples of leading and following swimming *C. c. bewickii* with chicks numbered at 77 and 73 birds, respectively. Finally, we considered 65 leading and 64 following swimming *C. cygnus* without chicks.

We used a binomial z-score to reveal the significance of the bias to keep the plane on the left or right side of the body and in the left or right visual field. Swimming leading and following *C. c. bewickii* and *C. cygnus* without chicks, swimming leading and following *C. c. bewickii* with chicks and flying leading and following *C. c. bewickii* without chicks were included in the analysis. The binomial z-score was calculated using the web-site https://www.socscistatistics.com/tests/binomial/default2.aspx. We used a chi-squared test to find differences in lateralisation bias in leading swimming and flying *C. c. bewickii* without chicks, following swimming and flying *C. c. bewickii* without chicks, leading swimming *C. c. bewickii* with and without chicks, as well as following swimming *C. c. bewickii* with and without chicks. Using a chi-squared test, we also compared the differences in behavioural lateralisation in swimming leading *C. c. bewickii* and *C. cygnus* without chicks and swimming following *C. c. bewickii* and *C. cygnus* without chicks. We used RStudio (ver. 4.1.4; R Core Team, 2021) for performing the chi-squared test and creating the graphs.

Results

Flying *C. c. bewickii* without chicks (Fig. 1a; Table 1) had a strong bias for keeping the source of disturbance on the left side and observing it by the left eye. A left side bias was found both in leading and following flying birds of *C. c. bewickii*. By contrast, the swimming *C. c. bewickii* without chicks had a right-side bias for keeping and observing the source of disturbance. Thus, the flying individuals tended to keep the plane on the left side and in their left visual field, while the swimming birds tended to keep the plane on the right side in their right visual field. The difference was significant for the flying and swimming leading birds without chicks (Chi-square test: $\chi^2 = 8.84$, $p = 0.003$) and for the flying and swimming following birds without chicks as well (Chi-square test: $\chi^2 = 10.73$, $p = 0.001$).

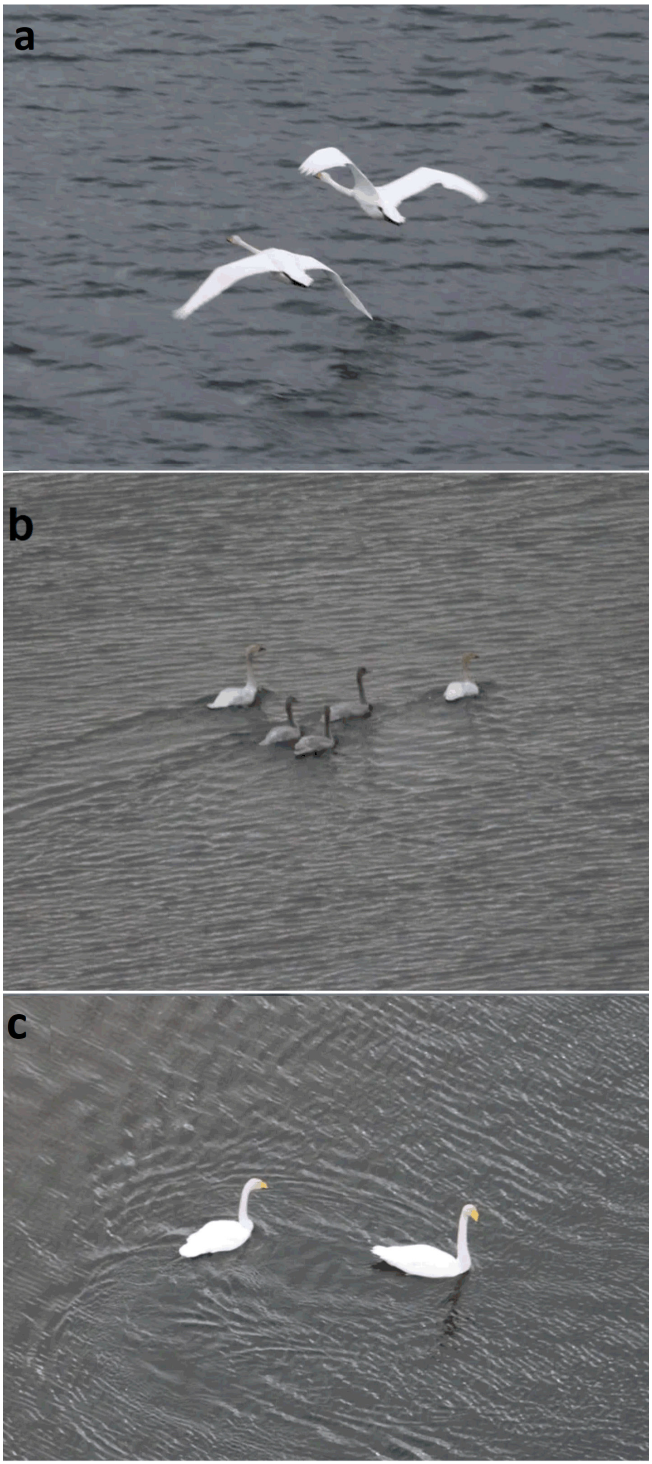

Fig. 1. Behavioural lateralisation when escaping from a disturbance source in various species and under different conditions. Designations: a – flying *Cygnus cygnus* keep the plane on their left side and in their left visual field; b – swimming *Cygnus columbianus bewickii* with chicks keep the plane on their right side and in their right visual field; c – swimming *Cygnus cygnus* without chicks keep the plane on their right side and in their right visual field.

The swimming *C. c. bewickii* with chicks (Fig. 1b), similar to the birds of the same species without chicks, showed a strong preference for keeping the plane on their right side and in their right visual field. The same trend was observed for the leading and following birds. No differences between birds with chicks and without chicks were found for the leading birds (Chi-square test: $\chi^2 = 2.53$, p = 0.111). Nevertheless, the proportion of following birds keeping the source of disturbance on the right side and observing it with the right eye was higher for the birds with chicks than for the birds without chicks. A significant difference was found for the following partners with and without chicks (Chi-square test: $\chi^2 = 5.24$, p = 0.024). Consequently, the presence of chicks did not appear to change the behavioural biases of the swimming birds, but it seemed to increase a right-side bias for the following partners.

The swimming *C. cygnus* (Fig. 1c) manifested the same bias in keeping the threat on the right side and observing it with the right eye, as *C. c. bewickii*. The leading swimming individuals of *C. cygnus* and *C. c. bewickii* in pairs without chicks showed a significant preference for this type of lateralisation. The following birds manifested a similar trend, but it was not significant in *C. cygnus*, while it was significant in *C. c. bewickii*. Nevertheless, no differences between the species were found (Chi-square test: $\chi^2 = 0.17$, p = 0.680 for leading birds, and $\chi^2 = 0.19$, p = 0.659 for following birds) (Table 1; Fig. 2).

Table 1. Behavioural lateralisation towards a source of anthropogenic disturbance in swimming and flying pairs of *Cygnus cygnus* and *C. columbianus bewickii* with and without chicks

Species	Activity	Chicks	Position	Left	Right	Sum	Bias	z	p-value
C. c. bewickii	Flying	–	Leading	42	23	65	Left	+2.23	0.012
C. c. bewickii	Flying	–	Following	42	23	65	Left	+2.23	0.012
C. c. bewickii	Swimming	–	Leading	41	62	103	Right	-1.97	0.024
C. c. bewickii	Swimming	–	Following	39	65	104	Right	-2.45	0.007
C. c. bewickii	Swimming	+	Leading	21	56	77	Right	-3.87	< 0.001
C. c. bewickii	Swimming	+	Following	15	58	73	Right	-4.92	< 0.001
C. c. bewickii	Swimming	+	Following	15	58	73	Right	-4.92	< 0.001
C. cygnus	Swimming	–	Leading	23	42	65	Right	-2.23	0.012
C. cygnus	Swimming	–	Following	27	37	64	No	-1.12	0.130

Note: z – binomial z-score. Designations: «Left» is a significant bias for keeping the plane on the left side and observing the plane with the left eye ($p < 0.05$); «Right» is a significant bias for keeping the plane on the right side and observing the plane with the right eye ($p < 0.05$).

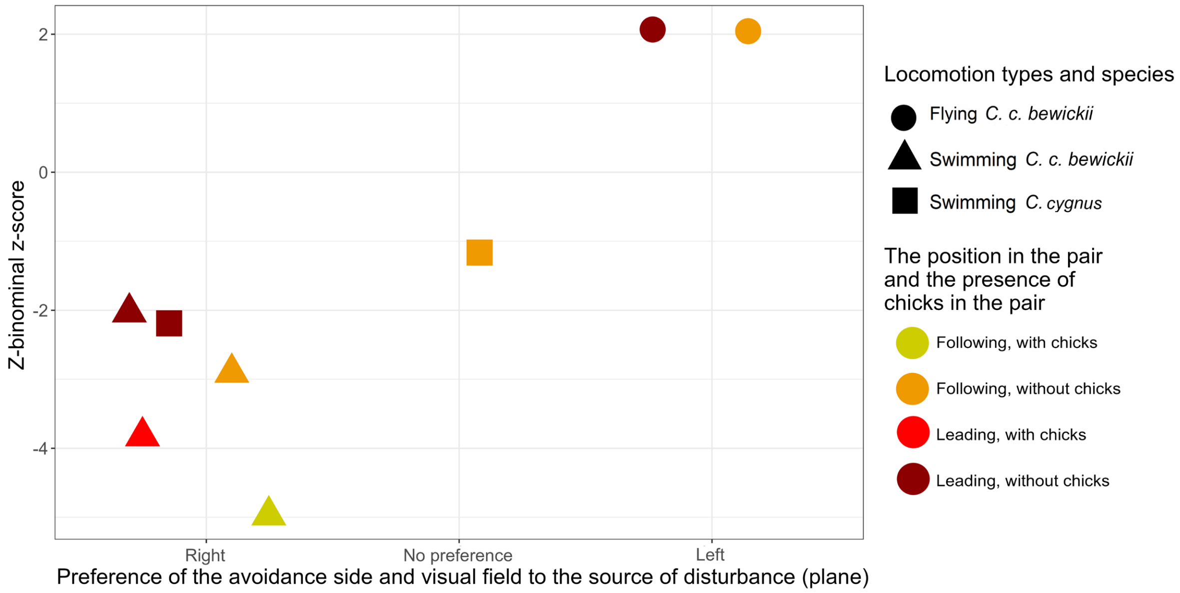

Fig. 2. The z-score of the preference to keep the source of danger (plane) on a certain side and use a certain eye for observing the threat. Designations: «Left» is a significant bias for keeping the plane on the left side and observing the plane with the left eye ($p < 0.05$); «No preference» is no lateralisation ($p > 0.05$); «Right» is a significant bias for keeping the plane on the right side and observing the plane with the right eye ($p < 0.05$).

Thus, the flying birds had a left bias in avoidance and observing the source of disturbance, while the swimming birds had a right bias. The right bias of swimming birds was consistent for *C. c. bewickii* and *C. cygnus*, for leading and following partners, and for birds with and without chicks.

Discussion

Our study has found that birds display opposite lateralisation when observing a disturbance source while swimming and flying. Swimming birds tend to keep the disturbance source on their right side and in the visual field of the right eye while flying birds tend to keep the disturbance source on their left side and in the visual field of the left eye. Previous studies on some gregarious species of birds found motor lateralisation while flying and swimming at the individual level, but no lateralisation at the population level (Mandel et al., 2008; Bhagavatula et al., 2014; Gutiérrez & Soriano-Redondo, 2020). Our findings contradict these results as we observed a significant behavioural bias at the population level. This difference could be attributed to the fact that in the previous studies the birds were avoiding obstacles while flying or feeding while swimming whereas in our study the birds were escaping from a source of danger while swimming or flying. Another possible reason is the high sociality of swans. Swans are social birds with long-term family bonds (Scott, 1980). A greater sociality is associated with higher lateralisation behaviour, as demonstrated in fish (King et al., 1998).

Swans in flight are likely to perceive the presence of a plane as a more threatening situation and experience greater fear than when they are on the water. As a result, the right hemisphere of the brain might be more active, and the source of disturbance is monitored with the left eye. It has been demonstrated that *Gymnorhina tibicen* have a left-eye bias when leaving a predator (Koboroff et al., 2008) or an approaching person (Hodges & Eldridge, 2001) and a right-eye bias when approaching a predator to study it during a state of low excitement (Koboroff et al., 2008). Another possible explanation is that swans in flight have to assess potential sources of danger faster and react to them immediately. The right hemisphere and left eye are often responsible for such tasks (Rogers & Kaplan, 2005, 2019; Rogers, 2010). This would be in line with other studies demonstrating that the left eye and right hemisphere are responsible for the observation of concrete threats (Rogers & Kaplan, 2005; Martín et al., 2010; Bonati et al., 2013) or threats located more closely (Zaynagutdinova et al., 2020). Additionally, the right hemisphere is also responsible for better orientation in space (Rogers, 2002), such as orientation relative to a plane. In contrast, swimming birds might perceive a plane as less dangerous and experience less fear. They are in a better position to determine which category the observed object belongs to and whether it will be dangerous. The left-hemisphere-right-eye system is responsible for scanning the environment when performing other tasks (Franklin & Lima, 2001; Randler, 2005; Beauchamp, 2013) and for determining a tiny difference in stimulus (Karenina & Giljov, 2022) that could be used in swimming.

Our analysis of swimming birds' behaviour showed the consistency of right-sided avoidance and a right-eye bias for this type of locomotion. Both leading and following partners demonstrated right-sided avoidance and a right-eye bias while swimming. The presence of chicks did not influence lateralisation in most cases but appeared to strengthen the lateralisation bias in the following partners.

No difference between the swan species was found in observing the disturbance source. Despite the fact that for following birds in *C. cygnus*, visual bias had the same tendency as for following birds in *C. c. bewickii*, but was non-significant. It is noteworthy that phylogenetically closely related species of swans had no significant differences in behavioural lateralisation in response to disturbance. This is contrary to previous findings on Passeriformes. The discrepancy might be due to the small sample size in the study of Franklin & Lima (2001). An alternative explanation is that behavioural lateralisation is more conservative in Anseriformes than in Passeriformes.

Our results suggest that conclusions on similar or opposite manifestations of motor and visual lateralisation in various species should only be made on the basis of studies with similar conditions. For example, a predator presentation test for visual lateralisation was conducted in similar experimental conditions in three species of toads, namely *Bufo bufo* Linnaeus, 1758, *Bufotes viridis* Laurenti, 1768, *Rhinella marina* Linnaeus, 1758, and revealed stronger escape or defense responses in all three species when the stimulus was on the toad's left side (Lippolis et al., 2002). Besides, in *Podarcis muralis* Laurenti, 1768 (Bonati et al., 2013), *Sminthopsis macroura*

Gould, 1845 (Lippolis et al., 2005), and *Gallus gallus domesticus* (Rogers, 2002), the same test also showed a stronger reaction to the predator when it was located in the left visual field. This may indicate the specialisation of a certain hemisphere for specific tasks. In our study, we could not separate motor lateralisation from visual lateralisation. However, it is important to study the manifestation of these types of behavioural biases separately.

As the behavioural bias was the same for the two phylogenetically closely related species and for the following and leading partners, we can conclude that the type of locomotion could influence the manifestation of behavioural lateralisation. Therefore, special attention should be paid to the details when comparing the results of various studies conducted under different circumstances.

As anthropogenic disturbance affects animal behaviour in general and behavioural lateralisation in particular, behavioural responses to such disturbance should be studied primarily in threatened species. The left side bias shown by the flying birds in our study indicates that flying birds are more stressed than swimming ones. To avoid causing unnecessary stress to birds, our recommendation to everyone conducting surveys or research is that birds should not be forced to fly.

Conclusions

The locomotion type affects the direction of behavioural lateralisation in the observation of a disturbance source in swans. *Cygnus c. bewickii* had a left side bias in avoidance and observation of a source of disturbance while flying and a right bias while swimming. The right bias of swimming birds was consistent for leading and following partners in pairs, for birds with and without chicks, and for two species of swans, namely *Cygnus c. bewickii* and *C. cygnus*.

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References

Alonso Y. 1998. Lateralization of visual guided behaviour during feeding in zebra finches (*Taeniopygia guttata*). *Behavioural Processes* 43(3): 257–263. DOI: 10.1016/s0376-6357(98)00015-1

Austin N.P., Rogers L.J. 2014. Lateralization of agonistic and vigilance responses in Przewalski horses (*Equus przewalskii*). *Applied Animal Behaviour Science* 151: 43–50. DOI: 10.1016/j.applanim.2013.11.011

Beauchamp G. 2013. Foraging success in a wild species of bird varies depending on which eye is used for antipredator vigilance. *Laterality* 18(2): 194–202. DOI: 10.1080/1357650X.2011.648194

Baciadonna L., Zucca P., Samour J. 2022. Laterality preferences at rest and predatory behaviour of the Gyrfalcon (*Falco rusticolus*): An alpha predator of the sky. *Laterality* 27(1): 86–100. DOI: 10.1080/1357650X.2021.1958831

Beekman J., Koffijberg K., Wahl J., Kowallik K., Hall C., Devos K., Clausen P., Hornman M., Laubek B., Luigujoe L., Wieloch M., Boland H., Svazas S., Nilsson L., Stipniece A., Keller V., Gaudard C., Degen A., Shimmings P., Larsen B.H., Portolou D., Langendoen T., Wood K.A., Rees E.C. 2019. Long-term population trends and shifts in distribution of Bewick's swans *Cygnus columbianus bewickii* wintering in northwest Europe. *Wildfowl* Special Issue 5: 73–102.

Bellebaum J., Kruckenberg H. 2009. Impact of hunting: from escape distance to the loss of feeding area. In: *Goose Specialist Group 12th Meetin*g. Hölviken, Sweden. P. 11.

Bhagavatula P.S., Claudianos C., Ibbotson M.R., Srinivasan M.V. 2014. Behavioral lateralization and optimal route choice in flying budgerigars. *PLoS Computational Biology* 10(3): e1003473. DOI: 10.1371/journal.pcbi.1003473

BirdLife International. 2021. *Cygnus columbianus* (Europe assessment). In: *The IUCN Red List of Threatened Species 2021: e.T22679862A166191206*. Available from https://dx.doi.org/10.2305/IUCN.UK.2021-3.RLTS.T22679862A166191206.en

Black J.M. 2001. Fitness consequences of long-term pair bonds in barnacle geese: monogamy in the extreme. *Behavioral Ecology* 12(5): 640–645. DOI: 10.1093/beheco/12.5.640

Boiko D., Kampe-Persson H. 2012. Moult migration of Latvian whooper swans *Cygnus cygnus*. *Ornis Fennica* 89(4): 273–280.

Boiko D., Wikelski M. 2019. Moulting sites of Latvian Whooper Swan *Cygnus cygnus* cygnets fitted with GPS-GSM transmitters. *Wildfowl* Special Issue 5: 229–241. DOI: 10.1134/S1062359018070178

Bonati B., Csermely D., Sovrano V.A. 2013. Looking at a predator with the left or right eye: Asymmetry of response in lizards. *Laterality* 18(3): 329–339. DOI: 10.1080/1357650X.2012.673623

Charles A., Mercera B., Delfour F. 2021. Bottlenose dolphins' (*Tursiops truncatus*) visual and motor laterality depending on emotional contexts. *Behavioural Processes* 187: 104374. DOI: 10.1016/j.beproc.2021.104374

Davies M.N.O., Green P.R., 1991. Footedness in pigeons, or simply sleight of foot?. *Animal Behaviour* 42(2): 311–312. DOI: 10.1016/S0003-3472(05)80562-7

Dharmaretnam M., Rogers L.J. 2005. Hemispheric specialization and dual processing in strongly versus weakly lateralized chicks. *Behavioural Brain Research* 162(1): 62–70. DOI: 10.1016/j.bbr.2005.03.012

Earnst S.L. 1992. The Timing of Wing Molt in Tundra Swans: Energetic and Non-Energetic Constraints. *Condor* 94(4): 847–856. DOI: 10.2307/1369282

Fang L., Zhang J., Zhao Q., Solovyeva D., Vangeluwe D., Rozenfeld S.B., Lameris T., Xu Z., Bysykatova-Harmey I., Batbayar N., Konishi K., Moon O.K., He B., Koyama K., Moriguchi S., Shimada T., Park J., Kim H., Liu G., Hu B., Gao D., Ruan L., Natsagdorj T., Davaasuren B., Antonov A., Mylnikova A., Stepanov A., Kirtaev G., Zamyatin D., Kazantzidis S., Sekijima T. et al. 2020. Two distinct flyways with different population trends of Bewick's Swan *Cygnus columbianus bewickii* in East Asia. *Wildfowl* 6: 13–42.

Féret M., Bêty J., Gauthier G., Giroux J.F., Picard G. 2005. Are abdominal profiles useful to assess body condition of spring staging Greater snow geese?. *Condor* 107(3): 694–702. DOI: 10.1093/condor/107.3.694

Franklin W.E., Lima S.L. 2001. Laterality in avian vigilance: do sparrows have a favourite eye?. *Animal Behaviour* 62(5): 879–885. DOI: 10.1006/anbe.2001.1826

Friedmann H., Davis M. 1938. "Left-handedness" in parrots. *Auk* 55(3): 478–480.

Güntürkün O., Diekamp B., Manns M., Nottelmann F., Prior H., Schwarz A., Skiba M. 2000. Asymmetry pays: Visual lateralization improves discrimination success in pigeons. *Current Biology* 10(17): 1079–1081. DOI: 10.1016/S0960-9822(00)00671-0

Gutiérrez J.S., Soriano-Redondo A. 2020. Laterality in foraging phalaropes promotes phenotypically assorted groups. *Behavioral Ecology* 31(6): 1429–1435. DOI: 10.1093/beheco/araa101

Heppner F.H., Convissar J.L., Moonan D.E., Anderson J.G. 1985. Visual angle and formation flight in Canada Geese (*Branta canadensis*). *Auk* 102(1): 195–198. DOI: 10.2307/4086847

Hodges J.I., Eldridge W.D. 2001. Aerial surveys of eiders and other waterbirds on the eastern Arctic coast of Russia. *Wildfowl* 52: 127–142.

Jeffery G., Erskine L. 2005. Variations in the architecture and development of the vertebrate optic chiasm. *Progress in Retinal and Eye Research* 24(6): 721–753. DOI: 10.1016/j.preteyeres.2005.04.005

Karenina K., Giljov A. 2022. Lateralization in feeding is food type specific and impacts feeding success in wild birds. *Ecology and Evolution* 12(2): e8598. DOI: 10.1002/ece3.8598

King J.G., Cooper B.A., Ritchie R.J. 1998. Mixed-species Swan flocks migrating in East-Central Alaska. *Northwestern Naturalist* 79(3): 104–107. DOI: 10.2307/3536839

Koblik E.A., Redkin Ya.A. 2004. Basic list of goose-like (Anseriformes) of the world fauna. *Kazarka* 10: 15–46. [In Russian]

Koboroff A., Kaplan G., Rogers L.J. 2008. Hemispheric specialization in Australian magpies (*Gymnorhina tibicen*) shown as eye preferences during response to a predator. *Brain Research Bulletin* 76(3): 304–306. DOI: 10.1016/j.brainresbull.2008.02.015

Krakauer A.H., Blundell M.A., Scanlan T.N., Weschsler M.S., McCloskey E.A., Yu J.H., Patricelli G.L. 2016. Successfully mating male sage-grouse show greater laterality in courtship and aggressive interactions. *Animal Behaviour* 111: 261–267. DOI: 10.1016/j.anbehav.2015.10.031

Kruckenberg H., Bellebaum J., Wille V. 2008. Escape distances of staging Arctic geese along the flyway. *Vogelwelt* 129: 169–173.

Leliveld L.M., Langbein J., Puppe B. 2013. The emergence of emotional lateralization: evidence in non-human vertebrates and implications for farm animals. *Applied Animal Behaviour Science* 145(1–2): 1–14. DOI: 10.1016/j.applanim.2013.02.002

Levy J. 1977. The mammalian brain and the adaptive advantage of cerebral asymmetry. *Annals of the New York Academy of Sciences* 299: 264–272. DOI: 10.1111/j.1749-6632.1977.tb41913.x

Lippolis G., Bisazza A., Rogers L.J., Vallortigara G. 2002. Lateralisation of predator avoidance responses in three species of toads. *Laterality* 7(2): 163–183. DOI: 10.1080/13576500143000221

Lippolis G., Westman W., McAllan B., Rogers L. 2005. Lateralisation of escape responses in the stripe-faced dunnart, Sminthopsis macroura (Dasyuridae: Marsupialia). *Laterality* 10(5): 457–470. DOI: 10.1080/13576500442000210

Magat M., Brown C. 2009. Laterality enhances cognition in Australian parrots. *Proceedings of the Royal Society B: Biological Sciences* 276: 4155–4162. DOI: 10.1098/rspb.2009.1397

Mainguy J., Bêty J., Gauthier G., Giroux J.F. 2002. Are body condition and reproductive effort of laying greater snow geese affected by the spring hunt?. *Condor* 104(1): 156–161. DOI: 10.1093/condor/104.1.156

Mandel J.T., Ratcliffe J.M., Cerasale D.J., Winkler D.W. 2008. Laterality and flight: concurrent tests of side-bias and optimality in flying tree swallows. *PLoS ONE* 3(3): e1748. DOI: 10.1371/journal.pone.0001748

Martín J., López P., Bonati B., Csermely D. 2010. Lateralization when monitoring predators in the wild: A left eye control in the Common Wall Lizard (*Podarcis muralis*). *Ethology* 116(12): 1226–1233. DOI: 10.1111/j.1439-0310.2010.01836.x

Mench J.A., Andrew R.J. 1986. Lateralization of a food search task in the domestic chick. *Behavioral and Neural Biology* 46(2): 107–114. DOI: 10.1016/S0163-1047(86)90570-4

Nice M.M. 1962. Development of behavior in precocial birds. *Transactions of the Linnaean Society of New York* 8: 1–211.

Pennycuick C.J., Einarsson O., Bradbury T.A.M., Owen M. 1996. Migrating Whooper Swans *Cygnus cygnus*: satellite tracks and flight performance calculations. *Journal of Avian Biology* 27(2): 118–134. DOI: 10.2307/3677141

R Core Team. 2021. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Available from http://www.R-project.org

Randler C. 2005. Eye preference for vigilance during feeding in coot *Fulica atra*, and geese *Anser anser* and *Anser cygnoides*. *Laterality: Asymmetries of Body, Brain and Cognition* 10(6): 535–543.

Rashid N., Andrew R.J. 1989. Right hemisphere advantage for topographical orientation in the domestic chick. *Neuropsychologia* 27(7): 937–948. DOI: 10.1016/0028-3932(89)90069-9

Red Data Book of the Russian Federation. Animals. Moscow: VNII Ecologiya, 2021. 1128 p. [In Russian]

Riddington R., Hassall M., Lane S.J., Turner P.A., Walters R. 1996. The impact of disturbance on the behaviour and energy budgets of Brent Geese *Branta b. bernicla*. *Bird Study* 43(3): 269–279. DOI: 10.1080/00063659609461019

Rogers L.J. 2002. Advantages and disadvantages of lateralization. In: L.J. Rogers, R.J. Andrew (Eds.): *Comparative vertebrate lateralization*. New York, USA: Cambridge University Press. P. 126–153. DOI: 10.1017/CBO9780511546372.006

Rogers L.J. 2010. Relevance of brain and behavioural lateralization to animal welfare. *Applied Animal Behaviour Science* 127(1–2): 1–11. DOI: 10.1016/j.applanim.2010.06.008

Rogers L.J., Kaplan G. 2005. An eye for a predator: Lateralization in birds with particular reference to the Australian Magpie. In: Y. Malashichev, A.W. Deckel (Eds.): *Behavioural and Morphological Asymmetries in Vertebrates*. Georgetown: Landes Boiscience. P. 47–57.

Rogers L.J., Kaplan G. 2019. Does functional lateralization in birds have any implications for their welfare?. *Symmetry* 11(8): 1043. DOI: 10.3390/sym11081043

Rogers L.J., Workman L. 1993. Footedness in birds. *Animal Behaviour* 45(2): 409–411. DOI: 10.1006/anbe.1993.1049

Rogers L.J., Zucca P., Vallortigara G. 2004. Advantages of having a lateralized brain. *Proceedings of the Royal Society B: Biological Sciences* 271(Suppl.6): 420–422. DOI: 10.1098/rsbl.2004.0200

Rogers L.J., Vallortigara G., Andrew R.J. 2013. *Divided brains: the biology and behaviour of brain asymmetries*. New York: Cambridge University Press. 229 p.

Rogers L.J., Koboroff A., Kaplan G. 2018. Lateral asymmetry of brain and behaviour in the zebra finch, *Taeniopygia guttata*. *Symmetry* 10(12): 679. DOI: 10.3390/sym10120679

Scott D.K. 1980. Functional aspects of the pair bond in winter in Bewick's swans (*Cygnus columbianus bewickii*). *Behavioral Ecology and Sociobiology* 7(4): 323–327. DOI: 10.1007/BF00300673

Syroechkovski E.E. 2002. Distribution and population estimates for swans in the Siberian Arctic in the 1990s. *Waterbirds* 25: 100–113.

Vallortigara G., Rogers L.J. 2020. A function for the bicameral mind. *Cortex* 124: 274–285. DOI: 10.1016/j.cortex.2019.11.018

Vallortigara G., Versace E. 2017. Laterality at the neural, cognitive, and behavioral levels. In: J. Call, G.M. Burghardt, I.M. Pepperberg, C.T. Snowdon, T. Zentall (Eds): *APA Handbook of Comparative Psychology: Basic Concepts, Methods, Neural Substrate, and Behavior*. Washington: American Psychological Association. P. 557–577. DOI: 10.1037/0000011-027

Vallortigara G., Cozzutti C., Tommasi L., Rogers L.J. 2001. How birds use their eyes: Opposite left-right specialization for the lateral and frontal visual hemifield in the domestic chick. *Current Biology* 11(1): 29–33. DOI: 10.1016/S0960-9822(00)00027-0

Vallortigara G., Chiandetti C., Sovrano V.A. 2011. Brain asymmetry (animal). *Wiley Interdisciplinary Reviews: Cognitive Science* 2(2): 146–157. DOI: 10.1002/wcs.100

Vangeluwe D., Rozenfeld S.B., Volkov S.V., Kazantzidis S., Morosov V.V., Zamyatin D.O., Kirtaev G.V. 2018. Migrations of Bewick's swan (*Cygnus bewickii*): new data on tagging the migration routes, stopovers, and wintering sites. *Biology Bulletin* 45(7): 706–717. DOI: 10.1134/S1062359018070178

Vince M.A. 1964. Use of the feet in feeding by the Great Tit *Parus major*. *Ibis* 106(4): 508–529. DOI: 10.1111/j.1474-919X.1964.tb03730.x

Workman L., Andrew R.J. 1986. Asymmetries of eye use in birds. *Animal Behaviour* 34(5): 1582–1584. DOI: 10.1016/S0003-3472(86)80235-4

Zaynagutdinova E., Karenina K., Giljov A. 2020. Lateralization of vigilance in geese: influence of flock size and distance to the source of disturbance. *Biological Communications* 65(3): 252–261. DOI: 10.21638/spbu03.2020.305

Zaynagutdinova E., Karenina K., Giljov A. 2021. Lateralization in monogamous pairs: wild geese prefer to keep their partner in the left hemifield except when disturbed. *Current Zoology* 67(4): 419–429. DOI: 10.1093/cz/zoaa074

ПОВЕДЕНЧЕСКАЯ ЛАТЕРАЛИЗАЦИЯ ЛЕБЕДЕЙ В ОТВЕТ НА АНТРОПОГЕННОЕ БЕСПОКОЙСТВО РАЗЛИЧАЕТСЯ В ЗАВИСИМОСТИ ОТ ТИПА ЛОКОМОЦИИ

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Численность европейской популяции *Cygnus columbianus bewickii* в последние десятилетия неуклонно снижается. Антропогенное беспокойство может быть одной из причин наблюдаемого снижения численности. Оно влияет на поведение животных, включая поведенческую латерализацию, поэтому информация о влиянии антропогенного беспокойства на поведенческую латерализацию имеет значение для сохранения биоразнообразия. Поведенческая латерализация проявляется в предпочтении использовать один из парных органов (конечности или сенсорные органы) и в предпочтении обходить препятствия с определенной стороны. Предыдущие исследования поведенческой латерализации не включали тип локомоции, как независимый фактор в анализ, однако он может влиять на поведенческую латерализацию. Таким образом, поведенческая латерализация может подвергаться влиянию различных факторов, которые следует учитывать при выполнении исследования. Мы изучили влияние антропогенного беспокойства на поведенческую латерализацию лебедей в зависимости от типа локомоции (плавания и полета). Мы проанализировали 492 фотографии с аэрофотосъемок двух видов лебедей: *Cygnus columbianus bewickii* и *Cygnus cygnus* на полуостровах Ямал и Гыдан. Фотографии были сделаны с самолета, в то время, когда птицы избегали его как источник антропогенного беспокойства. Встречались как одиночные пары без птенцов, так и с птенцами. Пары птиц могли быть также в стаях. Птицы плыли по воде или летели в небе. Мы обнаружили, что плавающие лебеди чаще держали источник антропогенного беспокойства справа от себя и наблюдали за ним правым глазом. Лебеди в полете, напротив, чаще держали источник антропогенного беспокойства слева от себя и в поле зрения левого глаза. Наличие птенцов значимо не влияло на поведенческую латерализацию, но усиливало ее. *C. c. bewickii* и *C. cygnus* проявляли сходную поведенческую латерализацию, когда плыли. Эти результаты были одинаковыми, как для ведомых, так и для ведущих птиц. Разница в поведенческой латерализации летящих и плывущих птиц может быть вызвана тем, что лебеди в полете испытывают больший страх от наличия самолета, чем когда они находятся на воде. Мы считаем, что тип локомоции влияет на поведенческую латерализацию по отношению к антропогенному беспокойству, поэтому при сравнении результатов исследований по латерализации поведения мы рекомендуем обращать внимание на сопутствующие факторы, в том числе и на тип локомоции животных. Поскольку летящие птицы держали самолет слева от себя и в поле зрения левого глаза, что указывает на то, что летящие птицы испытывают больший стресс, чем плывущие, мы рекомендуем обращать внимание при проведении исследований на методы и расстояние до животных и не допускать взлета птиц, чтобы не стрессировать животных во время учетов.

Ключевые слова: *Cygnus columbianus bewickii*, *Cygnus cygnus*, беспокойство, визуальная латерализация, моторная латерализация, плавание, полет, полуостров Ямал, полуостров Гыдан, птенцы

NUMENIUS ARQUATA (CHARADRIIFORMES, AVES) ABUNDANCE TRENDS IN AGROLANDSCAPES IN THE SOUTHERN REPUBLIC OF KARELIA (NORTHWEST RUSSIA)

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Olonets grasslands (61.041111° N, 32.931389° E) are the most extensive agrolandscapes in the Republic of Karelia (Northwest Russia), one of the largest spring stopovers of migrating birds in Northern Europe and a breeding area of farmland-associated birds. This territory is essential for the life of many bird species and is listed among international-level Important Bird and Biodiversity Areas of Russia. However, the preservation level of Olonets grasslands is rather low, since only spring hunting has been prohibited in a part of the Olonets grasslands (49 km^2) since 1993. Thus, the conservation status of this area and the bird protection measures have to be upgraded and a system should be set up for monitoring the abundance of Red Data Book and other threatened species, which use this territory in certain stages of their life cycle. One of such species is *Numenius arquata* (hereinafter – curlew), many populations of which have both declining abundance and shrinking distribution. This species uses the Olonets grasslands both as a spring migration stopover and as a breeding area. We analysed the curlew registrations obtained in the Olonets grasslands in April and May 1997–2023 during the transect censuses (both transect walks and surveys using a car). We compared these records with both local weather data and grassland use intensity. We also analysed the time dependence of curlew spring abundance on date and year of observations. The research hypothesis was that curlew's abundance decreased in cold spring seasons, in seasons with intensive grassland use, as well as over time. The latter supposition is based on the observations of a curlew population decline in the past decades in various parts of the species' range. The monitoring showed that this species is consistently present in the Olonets grasslands in April – May. Curlews, stopping over on migration, used the grasslands quite evenly, with no clear preference for any specific areas. In the case of breeding, however, they tended to choose the sites most inconvenient for agricultural treatments. The even distribution of curlews over the grasslands was probably due mostly to the individuals foraging in stopovers. In the surveyed part of the Olonets grasslands (49 km^2), the size of the local population breeding varied from 30 to 150 pairs in 1999–2023. In 2019–2023, it was 30–90 pairs. In the entire Olonets grasslands (180 km^2), the breeding curlew population varied from 100 to 1200 pairs at various years in 1999–2023, but it did not exceed 100–300 pairs in 2019–2023. During the stopping over on migration, the annual number of curlew individuals passing through the surveyed part of the Olonets grasslands was 90–750, while it was 150–2500 birds in the entire Olonets grasslands. So far, we have found no correlation between the total abundance of curlews in the study area and the intensity of grassland use, apparently because stopover and breeding sites are still available. On the other hand, the curlew abundance was lower in warmer spring seasons. Apparently, some curlews fly farther north in such seasons, whereas in colder seasons more birds settle on Olonets grasslands or linger on them on their migration route. Over 25-year retrospective, the total curlew abundance registered in the Olonets grasslands has decreased by 34.4%. In the study area, the negative trend in the species abundance was likely due not only to local but also to global processes, which have caused a decline in some other European populations as well. These birds probably face with certain problems on flyways or in wintering grounds, but more data are needed to verify this conjecture. The local-scope factors that may potentially affect curlew abundance include burning of last year's grass cover, farming intensification, predation, and human disturbance. By assessing possible future changes in the curlew abundance in the Olonets grasslands, we predict that in the coming 30–40 years this species is highly likely to become «endangered» in the study area. To prevent this from happening, it is necessary to conserve the sites where curlews can nest, strengthen the protection regime in the Olonets grasslands (preferably through designation of a high-status Protected Area), and raise public awareness of the need to conserve the species and reduce human disturbance.

Key words: agrolandscape, monitoring, Protected Area, protected species, wader

Introduction

Numenius arquata (Linnaeus, 1758) (hereinafter – curlew) is a wader species assessed by the International Union for Conservation of Nature (IUCN) under the Near Threatened (NT) status (BirdLife International, 2023). Some populations of the nominate subspecies, *N. a. arquata* (Linnaeus, 1758), are included in the Red Data Book of the Russian Federation (Sviridova, 2021) under the status «subspecies populations with a decreasing abundance and distribution» (vulnerable species, status in Russia under IUCN classification is VU (Vulnerable) in conservation priority class III). Accordingly, the curlew is listed in the Red Data

Books of most regions in the Russian Federation inhabited by populations of *N. a. arquata*. In Russia, it is protected in at least 40 Protected Areas (PAs) under various statuses (Sviridova, 2021).

In the last edition of the Red Data Book of the Republic of Karelia (2020), the status of the curlew, as a rare species, is 3(NT). It is worth noting that the Republic of Karelia is located at the northern periphery of the species' range, but since the mid-XX century data have been accumulating that the curlew has been expanding its distribution northwards along the western coast of the White Sea (Lappo et al., 2014). At the same time, as stated in the literature, there is a strong deficit of data on the biology of *N. a. arquata* in the north of its range in general (Lappo et al., 2014) and in its Russian part in particular (Douglas, 2020). Thus, the relevance for monitoring of the curlew abundance in the Republic of Karelia arises from the following: (1) poor status of some *N. a. arquata* populations, (2) overall instability of peripheral populations, (3) importance of collecting data on species, distribution of which is changing, (4) poor knowledge of the *N. a. arquata* biology in the north of the Russian part of its range. Since all these aspects are of global importance, data on the curlew in the Republic of Karelia will be wanted both in Russia and abroad.

The monitoring of the *N. a. arquata* abundance in farmlands is important. Although apart from agrolandscapes curlews can nest in wet meadows and marshes, the farmlands are habitats occupied by *N. a. arquata* in the Republic of Karelia at the highest abundance (Zimin et al., 1998; Lapshin et al., 2012; Khokhlova et al., 2023). In 1990–2010, *N. a. arquata* individuals have reportedly been settling in farmlands more often in general than before (Sviridova, 2014). Besides, they actively use farmlands for extensive movements during the breeding period and migration (Zimin et al., 1998; Sviridova, 2021; Khokhlova et al., 2023).

In the Republic of Karelia, Lehtonen (1943) conducted the first studies to provide, among other things, data on the biology of the curlew. Among other results, Lehtonen (1943) found a more accurate delineation of the breeding range of the curlew in the Republic of Karelia. The first summarising review, focusing specifically on the avifauna in the southern Republic of Karelia, was produced by Neifeldt (1958) using data from the literature and original material collected during field trips in 1954–1955. Later, Zimin & Ivanter (1974) carried out extensive avifaunal research covering also the southern Republic of Karelia. These studies were then continued (Zimin et al., 1993, 1998; Artemyev et al., 2016).

Since 1993, spring bird aggregations have been studied in the Olonets grasslands. These data have been partially published, including some data on the curlew (e.g. Zimin et al., 2007; Lapshin et al., 2012; Artemyev et al., 2021; Khokhlova et al., 2023). However, most of the publications based on material from the Olonets grasslands are concerned to Anseriformes (e.g. Artemyev et al., 2009, 2019, 2020, 2022). The pool of data on the curlew in the Olonets grasslands has not yet been fully processed and synthesised.

The aim of this paper was to summarise and analyse data on the curlew abundance dynamics in the Olonets grasslands, southern Republic of Karelia, collected during a special monitoring in 1999–2023. For this purpose, we performed the following tasks: (1) collecting data on the abundance of curlews breeding in the Olonets grasslands and those using this area to stop over on migration; (2) analysing the collected data, including the correlations between abundance trends and selected factors. The working hypothesis was that the abundance of curlews decreased in colder spring seasons, at times of more intensive grassland use, as well as over time. The latter supposition is based on the observations of curlew abundance declining in the past decades in various parts of the species range (Douglas, 2020; Sviridova, 2021; BirdLife International, 2023). Additionally, we have planned to assess possible changes in the curlew abundance in the study area depending on the spring hunting pressure. Curlews are not a hunting target in the area, but they may be disturbed when birds of other species are hunted.

Material and Methods

Study area and methods

We conducted field surveys in 1999–2023 in farmlands in the Olonets district in the Republic of Karelia (Northwest Russia), situated near the town Olonets (Fig. 1), i.e. so-called Olonets grasslands (61.041111° N, 32.931389° E), as the most extensive agrolandscapes in the Republic of Karelia, covering about 180 km^2. Olonets grasslands are one of the largest spring stopovers of migrating birds in Northern Europe and a breeding area of many farmland-associated birds (Zimin et al., 2007). By considering the essential role in the life of many birds, the Olonets grasslands were listed among international-level Important Bird and Biodiversity Areas of Russia (http://www.rbcu.ru/programs/93/).

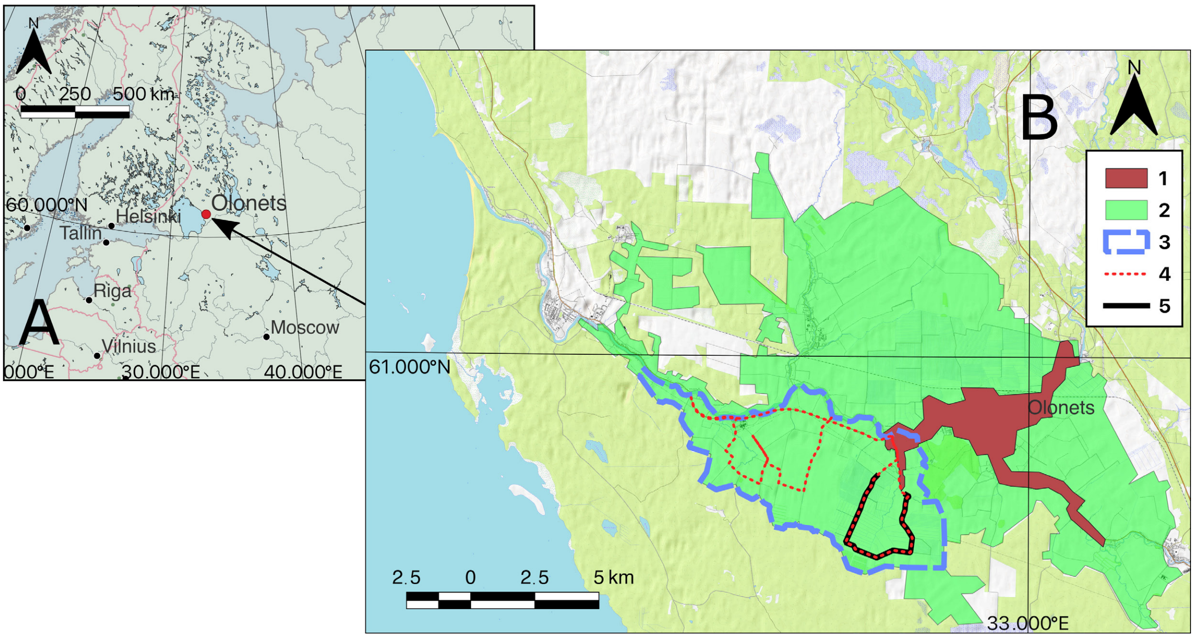

Fig. 1. The location of the study area and its key elements. Designations: A – the town Olonets on the map of Europe, B – key elements in the study area; 1 – the town Olonets and adjacent settlements, 2 – farmlands around the town Olonets, 3 – «Non-hunting zone» seasonal sanctuary, 4 – long-term car survey route, 5 – long-term walking survey route.

Over the study period, the situation for birds in the farmlands has changed, i.e. the conditions of the Olonets grasslands have improved considerably: reclamation channels were deepened; drainage pipes were cleaned; trees and shrubs were cut along the field edges. Besides, in the late XX century, the Olonets grasslands were predominantly covered in degenerating perennial grasses, whereas grain and row crops occupied less than 5% of the study area. During the XX century, the farmlands have been exploited more intensively; perennial grasses have been timely renewed; the proportion of grain and legume crops increased up to 15–20%. With the agriculture intensification, the anthropogenic pressure on birds increased accordingly (Zimin et al., 2007; Artemyev et al., 2022).

Being located on highly wet soils, the Olonets grasslands are covered by a net of reclamation channels. Their shores are being densely overgrown with shrub vegetation, represented predominantly by *Salix* sp. Their thickets are cut down periodically. At the end of the winter, strong winds blow snow off by opening the fields' surface. When snow begins melting, water accumulates in depressions. At Olonets grasslands' elevations devoid of snow, thawing of the upper soil layers begins earlier than in typical taiga habitats (Zimin et al., 2007).

In the study area, the spring hunting lasts normally ten days, usually at 01–10 May. However, in 1993, a 49 km^2 area of the Olonets grasslands (Fig. 1) was declared a termless local-scope seasonal sanctuary called the «Non-hunting zone». The conservation status of this area changed several times from a municipal-level sanctuary with a special protection regime to one, which has not any protection regime. After losing its Protected Area's status (in 1996), this part of the Olonets grasslands was no longer subject to a special protection regime but retained the «Non-hunting zone» status, so bird hunting is prohibited there in spring (Artemyev et al., 2022).

Additionally, the Olonets grasslands had for a long time been cleared by burning of last year's herbaceous vegetation. There is no custom of mowing after-grass there. Therefore, the dry grass has been burnt down in spring, including the protected parts of the fields. Burning of the after-grass started after its drying up, which depended on the spring weather. Therefore, the after-grass burning began in mid-April or in the third decade of April, by sometimes continuing until mid-May. In the Olonets district, all farming enterprises annually burn out 60–80% (about 55% on average) of their grassland areas (Zimin et al., 2007; Artemyev et al., 2022). The practice of after-grass burning in the grasslands was terminated in 2014 and not resumed later, although this practice has been used again in part of the Olonets grasslands in 2023.

A detailed description of the study area and methods was published in Zimin et al. (2007). The main sampling method was walking transect surveys. The walking survey route (9.5 km long) was along a road passing through farmlands typical in the Olonets district (Fig. 1). Fields with sown perennial grasses prevailed there, while areas of grain crop stubble or arable fields were less frequent. There were brooks flowing through the fields and a developed net of reclamation channels, which are usually full with water in April and early May. Surveyors walked the route in the morning, starting at 6:00–8:00 depending on the weather. As a rule, each survey tour took around 4 h. We counted curlews in strips (up to 50 m, 50–100 m, and 100–150 m wide) by registering individual birds, migrating aggregations and local pairs. The counting of birds by stripes provided the possibility of counting the number of birds per area. In 1999–2009, the routes were walked daily, and each other day since 2010.

An additional method was car transect surveys, meaning that a certain route through the Olonets grasslands (in total, 39.5 km), partially coincident with the walking transect (Fig. 1), was toured by cars during daytime (usually at 15:00–18:00). This way, we separately recorded local and migrating curlews to the maximum detectability distance. To design the car transect, we took into account data on the best possible view-ability of the studied area using binoculars from aboard the car. The conversion of the bird abundance per unit area was based on the area of plots viewed. The car surveys were usually toured daily, but in 2010, 2011, 2012, 2016, and in May 2017, they were conducted each other day. In 2018, 2019 and 2023, car transect surveys were conducted daily during the peak migration time, and every other day in the rest part of the study period every season.

To analyse the obtained data, we used material gathered in the Olonets grasslands from 21 April to 19 May in 1999–2019 and 2023. The studied area of the fields covered almost the entire «non-hunting zone», and accounted for about 20% of the total area of the Olonets grasslands (Fig. 1).

Data analysis

The analysis was based on the absolute abundance of curlews registered on the counting routes. To allow us to compare those with data from other areas, we converted the absolute abundance of bird individuals to the relative abundance. The main studied parameter was the relative total abundance of resident and migrating curlew individuals recorded in the Olonets grasslands. The additional considered parameters were the maximal daily abundance and the peak abundance date in the form of the total number of monitoring days since the beginning of the year. When comparing the data collected by various methods, considering that the car transect (39.5 km) was much longer than the walking transect (9.5 km), we used the material from the 9.5-km long model section of the transect covered by both walking and car surveys (Fig. 1).

To estimate the curlew abundance in the studied part of the Olonets grasslands, we used data from both walking and car surveys. However, when extrapolating data on the bird abundance to the total area of the Olonets grasslands, we used the data from the walking surveys only as providing more accurate information. At the same time, we did not re-calculate the entire area of agrolandscapes (180 km^2), but only the area of sites suitable for nesting and stopovers of curlews (with a total area of 84.7 km^2), excluding too moisturised sites, roads, and sites overgrown with shrubs or occupied by vegetable gardens.

We analysed temperature effects on the total abundance of curlews using long-term data on air temperature data during the study period, which are openly available at https://rp5.ru. We used the temperature data (for 09:00 h) from the nearest weather station in the town Olonets. For calculations, we used the average values of the mean temperature for the period from 21 April to 19 May.

We analysed the use intensity of the Olonets grasslands on the model area surveyed with the walking transects using QGIS 3.30.2 Hertogenbosch software (QGIS.org, 2022), Google Earth Engine and Google Earth Engine Data Catalog plugins with an open access to historical Landsat 4, 5, 7, 8, and 9 satellite images (Gorelick et al., 2017). As an indicator of the Olonets grasslands use intensity, we used the proportion of cultivated farmlands on the basis of satellite imagery decoding. Data on bird abundance in relation to the spring hunting have been classified into three categories: period before the opening of the hunting season (before 01 May), period of the hunting season (01–10 May), and period after the closing of the hunting season (after 10 May).

The classifying of curlew individuals, feeding on the Olonets grasslands, to local breeding and migrant birds was difficult. The gregarious behaviour of the migrating birds at the stopovers was the main criterion for this purpose. To compensate a possible undercounting of the number of migrating curlew individuals, we applied the following formula to refine the classification during ex situ treatment of data for each study season:

$$N_{tr} = \frac{\sum_{x \in C}(\max Q_4 - E(Q_3))}{N_{all}} \times 100\%,$$

where N_{tr} – the percentage of migrant individuals, C – groups of consecutive surveys between days with below-median values of the bird abundance, $\max Q_4$ – the maximal value in C groups within the fourth quartile, $E(Q_3)$ – the borderline maximal value of third quartile, N_{all} – the total number of counted birds.

To compare the rate of changes in bird abundance over the study period, we used the following formula:

$$\Delta N = \frac{Me_{start} - Me_{end}}{Me_{start}} \times 100\%,$$

where ΔN – the rate of changes in bird abundance, Me_{start} – the median of the total bird abundance in the first five study seasons, Me_{end} – the median of total bird abundance in the last five study seasons.

All calculations were performed using the R v. 4.1.1 programming environment (R Core Team, 2021), and using RStudio 2021.09.1 Build 372 as the graphical shell (RStudio Builds, 2021). The obtained data series were tested for normality using the Shapiro-Wilk test and for being outlier-free using an «outliers» package (Komsta, 2022). Since most of the data series had a non-normal distribution, in most cases we chose the median as the measure of central tendency and the interquartile range as the measure of dispersion. For temperature indicators, we calculated an average value.

We analysed relationships between data series using Spearman's rank correlation and conducted comparisons between them using the Wilcoxon test for paired samples. To describe the dynamics of numerical attributes, we selected models using the «basicTrendline» package (Mei & Yu, 2020). Before constructing the abundance dynamics models, we tested the data series for autocorrelation in the R software (R Core Team, 2021) using the «acf» function with the lag ranging from 1 to the sample set length. During data pre-treatment, we considered the possibility of abundance parameters being influenced by the number of surveys. The number of surveys within the given time interval varied among years. But we detected no significant correlations between bird abundance in the Olonets grasslands and the number of surveys (Spearman's rank correlation, Rs = 0.38, p = 0.09).

Results

In late April – May of each year, curlews visited the Olonets grasslands at a total density of 0.4–18.0 individuals per 1 km^2 (ind./km^2). The majority of the registered birds (73.8% median, varying from 40.0–90.6% among years) were migrants, which used the Olonets grasslands as a stopover. The others were local breeding birds. Curlews mostly appeared in the Olonets grasslands in mixed flocks with *Numenius phaeopus* (Linnaeus, 1758) or in small single-species flocks formed by several individuals to several dozen birds or, rarely, by several hundred individuals.

In 1999–2023, the abundance of curlews observed in one day on a walking transect varied from 3–153 individuals per route (9.5 km). On a complete car route (39.5 km), we daily recorded from several individuals to 460 birds. In 1999–2023, the size of the local bird population breeding in the thoroughly surveyed part of the Olonets grasslands (49 km^2) varied from 30–150 pairs per season. In 2019–2023, it was 30–90 pairs per season. We extrapolated these data to the entire area of the Olonets grasslands (180 km^2), keeping in mind their inhomogeneity and varying suitability for breeding and staging of curlews. As a result, we found that the size of the entire Olonets grasslands' breeding curlew population in 1999–2023 can be estimated at 100–1200 pairs depending on the year. We found that its size was 100–300 pairs per season in 2019–2023. The annual number of curlews migrating through the surveyed part of the Olonets grasslands was 90–750 individuals, and the estimated number of individuals on the entire area of the Olonets grasslands was 150–2500 birds.

When the curlews stayed in the Olonets grasslands, generally suitable for them as breeding and stopover sites, these birds occupied this territory quite evenly, without clear preference for certain zones. This is confirmed by our results that the bird density was nearly equal in various sampling strips easily viewable with binoculars (Fig. 2). According to our observations, when choosing the nesting sites, most curlew individuals prefer sites, which are most inconvenient for agricultural treatments.

The species' abundance trends remained relatively stable year-to-year throughout the study period (Fig. 3). The basis of the stationary group was formed predominantly by individuals occupying the Olonets grasslands for breeding. On the other hand, migrant individuals stopped over, changing one another. The most massive arrivals and departures were observed in April, with a gradual declining of migrating bird flows in May (Fig. 3).

Walking transect surveys revealed a steady decrease in the curlew abundance over the study period (Fig. 4). Over the 1999–2023 period, the dynamics of the median density values conformed to a linear model with the minimal Akaike information criterion (AIC) (Fig. 4). This model describes the variation of the interquartile range of values of the abundance of counted curlews (Fig. 5). Based on the walking transect surveys, the curlew abundance in the Olonets grasslands generally decreased over the 1999–2023 period by 34.4%. A predictive assessment of further potential changes in the bird abundance using models based both on median values (Fig. 4) and variability indices (Fig. 5) suggests that within the next 30–40 years the curlew can be highly likely recognised as an endangered species in the study area.

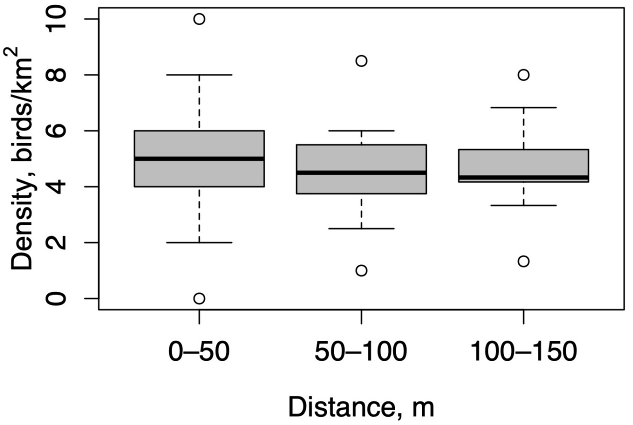

Fig. 2. The relative total abundance of curlews in various sampling strips based on results of walking transect surveys. The upper and lower borders of the boxes denote the first and third quartiles; «whiskers» denote the intervals, in which the vast majority of data fall, not exceeding the value of 1.5 interquartile range of values; the horizontal line denotes the median value; circles – outliers.

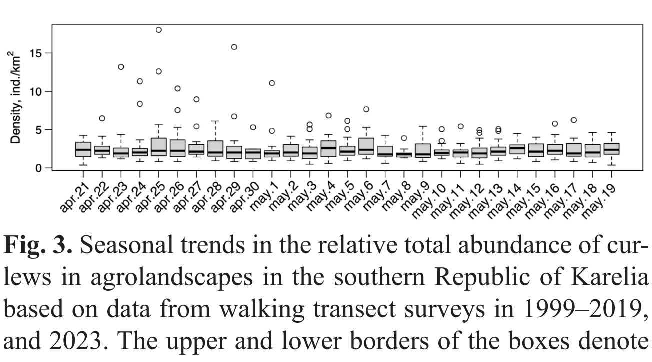

Fig. 3. Seasonal trends in the relative total abundance of curlews in agrolandscapes in the southern Republic of Karelia based on data from walking transect surveys in 1999–2019, and 2023. The upper and lower borders of the boxes denote the first and third quartiles; «whiskers» denote the intervals, in which the vast majority of data fall, not exceeding the value of 1.5 interquartile range of values; the horizontal line denotes the median value; circles – outliers.

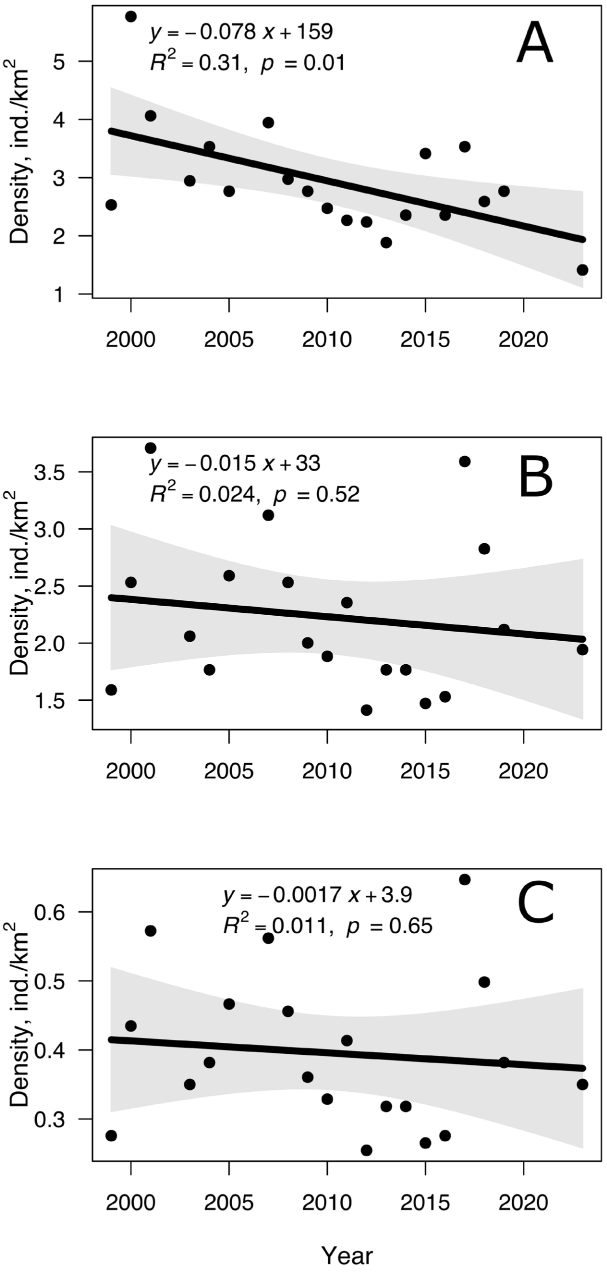

Fig. 4. Long-term trends in relative total abundance of curlews in agrolandscapes in the southern Republic of Karelia. Designations: A – based on the results of walking surveys at the 9.5 km long transect, B – based on the results of car surveys at the 9.5 km long transect section concurring with the walking transect, C – based on the results of car surveys at the 39.5 km long transect.

At the same time, car surveys of the same route surveyed during walking surveys (Fig. 1) revealed non-significant ($p = 0.52$) changes in the bird abundance, although the slope of the trend line also indicated a decline (Fig. 4). In general, the results obtained using car transect surveys on the model area, which was studied by both walking and car transect surveys, were in significant agreement with the results of walking transect surveys (Spearman's rank correlation: $Rs = 0.23$, $p < 0.01$), although the positive correlation was weak.

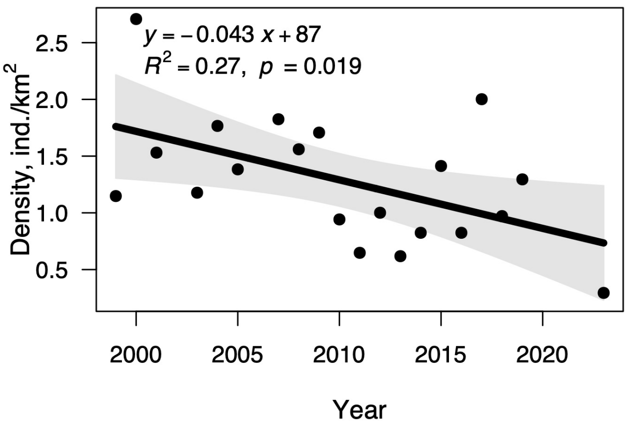

Fig. 5. Long-term variation of the interquartile range of values of the relative total abundance of curlews counted during walking transect surveys.

The dynamics of the relative total abundance of curlews was estimated based on the results of complete car transect surveys (Fig. 4). There were no regular patterns in the distribution of median values of the data series produced by car transect surveys. At the same time, the number of outliers in the data series from car surveys significantly exceeds the number of outliers in the data series from walking transect surveys (paired sample Wilcoxon test: $W_{20, 20} = 15$, p = 0.02).

The analysis of the correlation of the bird abundance to the temperature showed a significant negative correlation (p = 0.017) between the number of birds counted on the route and the mean values of air temperature during the observation period (Fig. 6). No correlation was found between the relative total abundance of curlews and Olonets grasslands' use intensity in either walking transect surveys (Spearman's rank correlation: Rs = -0.08, p = 0.75) or car transect surveys of the same routes (Spearman's rank correlation: Rs = -0.39, p = 0.09). We did not find any significant correlation between the migration passage rate (a day with the highest bird abundance) and Olonets grasslands' use intensity either (Spearman's rank correlation: Rs = 0.41, p = 0.07). Our analysis also showed that the spring bird hunting season had no significant effect on the curlew abundance in the «Non-hunting zone» (Fig. 7).

Discussion

Monitoring of the spring abundance of curlews in the Olonets grasslands in the southern Republic of Karelia in 1997–2023 proved that this species was constantly present there in late April – May. Pioneer individuals arrive in the area at 05–17 April (Khokhlova et al., 2023). We found that the migration period can last until mid-May. The vast majority of the observed birds (about three quarters of all counted curlews on average) were migrant individuals, which use the Olonets grasslands as a stopover site during the migration. Accordingly, the local breeding curlews, accounted for about a quarter of all observed birds. The even distribution of curlews in the Olonets grasslands during the study period was apparently caused mostly by birds stopping during the migration for feeding.

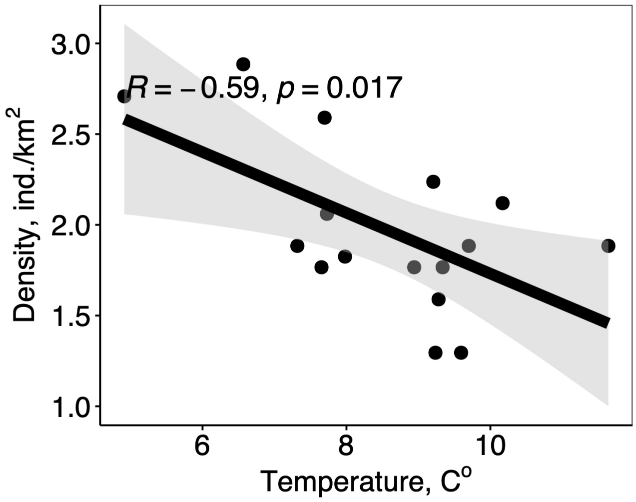

Fig. 6. The relationship between the relative total abundance of curlews and the mean air temperature over the annual sampling period based on data obtained at 9:00 from 21 April to 19 May in 1999–2023 (Pearson product-moment correlation).

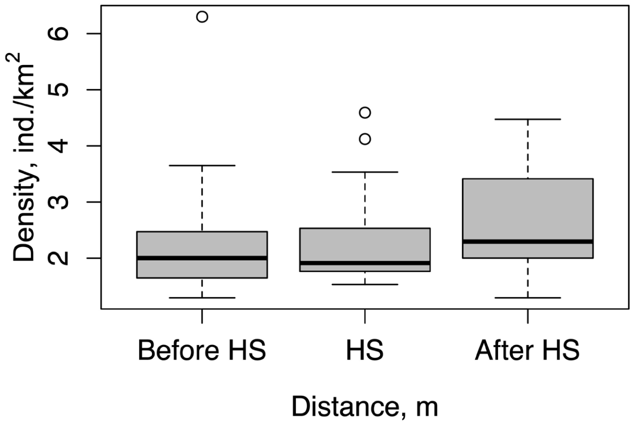

Fig. 7. The relative total abundance of curlews in the «Non-hunting zone» area before the opening of the hunting season in adjacent areas (Before HS), period of the hunting season (HS), and period after the closing the hunting season (After HS). The upper and lower borders of the boxes denote the first and third quartiles; «whiskers» denote the intervals, in which the vast majority of data fall, not exceeding the value of 1.5 interquartile range of values; the horizontal line denotes the median value; circles – outliers.

The breeding grouping of curlews in the Olonets grasslands can be considered quite large in European Russia. The density of curlew individuals using this area for breeding was even higher in the last years. For instance, 400–1200 curlew pairs were registered in the Olonets grasslands in late 1990s – early 2000s (Zimin et al., 2009). In the regions adjacent to the Republic of Karelia, Vologda Region (Butiev et al., 1998), Arkhangelsk Region (Butiev & Shitikov, 1998; Sviridova, 2020), and Leningrad Region (Noskov et al., 2016; Golovan & Khrabry, 2018), the curlew populations were relatively stable, but they did not form large breeding groups. In the Murmansk Region the curlew is rare (Noskov et al., 2016). In the centre of European Russia the abundance of breeding curlew groups is also relatively low; for instance, the size of breeding groups here varies from single pairs to several dozen pairs (e.g. Ivanchev, 2011; Tyulkin, 2012, 2020; Galchenkov, 2017; Bykov et al., 2018).

Our data on long-term trends in the abundance of the birds counted in the Olonets grasslands quite varied depending on the sampling method. The results of walking transect surveys pointed to a steady decline in the curlew abundance over the study period, whereas car transect surveys showed only a downward tendency in bird abundance, without any significant change. The lack of complete agreement between the curlew abundance indices produced by various methods can be caused by both the various time of the conducted surveys (walking transect surveys were performed in the morning, while car surveys during daytime) and the unequal performance of the various sampling methods in bird registration. We believe that the walking transect survey method more accurately represents the actual curlew abundance in the grasslands. This is indirectly evidenced by the fact that the bird density within various sampling strips was highly similar. In general, according to walking transect surveys, the total curlew abundance in the Olonets grasslands decreased by 34.4% over the 25 years.

On the other hand, the substantial length of the car transect, which is considerably longer than the walking transect, allows us a better chance to capture a short-term local rise in the bird abundance. This is also evidenced by the large number of outliers in the car survey data. As a rule, such local concentrations of birds were associated with the migration process. In addition to the migration, a short-term rise in bird density and appearance of actively moving individuals could be a consequence of mass destruction of nesting sites as a result of burning of the last-year's vegetation or other farmland treatments.

We also found a higher curlew abundance in colder spring seasons. A possible explanation is that in colder springs birds of northern curlew populations partially delay along the migration by migrating northwards at a later period. It is also likely that some curlew individuals in cold springs stay to nest southwards of their usual breeding sites, thus enlarging the size of local curlew population of the Olonets grasslands. However, both of these assumptions require further research. Regarding the influence of grassland use intensity, our data revealed no significant correlations of the curlew abundance with this factor. It appears that variations in the grassland use rate in the study have little impact on the breeding bird density of the curlew. For any type of observed exploitations, suitable nesting sites were retained in the Olonets grasslands. Even burning of the last year's vegetation allowed curlews to nest in the Olonets grasslands after the herbaceous cover had regenerated.

Thus, the decrease in the curlew abundance in the Olonets grasslands can hardly be attributed solely to the local conditions. Reasons for that should probably be sought in the situation along the entire migration ways and in wintering sites, as well as by comparing our findings with data from other regions used by the curlew. In European Russia, the abundance of nominate subspecies (*Numenius a. arquata*) decreased at least since 1970s–1990s (see Tomkovich & Lebedeva, 1998, 1999; Butiev, 2001). Since the 1980s, its decline was 5–30% (BirdLife International, 2015; Mishchenko et al., 2017). In many regions of European Russia, the curlew abundance continues declining, but in some areas its decrease has stopped in the early XXI century (Sviridova, 2021). In the northern European Russia, the curlew abundance has remained relatively stable in 2000–2020 (Noskov et al., 2016; Golovan & Khrabry, 2018; Sviridova, 2019, 2021). In southern regions of European Russia, however, especially in the Middle Volga Region, the bird abundance decreased considerably over 2000–2020 (Sviridova, 2021).

A more critical (than in European Russia) decrease in the curlew abundance has occurred in other European countries (BirdLife International, 2023; Rigal et al., 2023). In particular, a considerable decline of the curlew abundance was found in the United Kingdom (Harris et al., 2014; Hayhow et al., 2014), Ireland (Balmer et al., 2013; Booth Jones et al., 2022), and Estonia (Elts et al., 2013). Starting since the 1980s, a long-term decrease of this species' abundance has been observed in Norway, Sweden, and Finland, among which the curlew abundance has stabilised only in Finland in 2001–2012, whereas in Sweden and Norway its values are still declining (BirdLife International, 2015). A long-term abundance decline since the early 1980s has also been recorded in the Netherlands and Germany. The decline is still continuing in the Netherlands, while in Germany the curlew abundance became more stable (Hötker et al., 2007; BirdLife International, 2015). In some other European countries, a decrease in curlew abundance was also noted. In general, European population of the curlew decreased by 30–49% over the period 1980–2015. Thus, over 30 years, its European population lost around a third of its original size (BirdLife International, 2015).

In Central Asia, the decrease in abundance of the nominate subspecies has also been registered, while the abundance of breeding curlews in Eastern Siberia has likely remained stable (BirdLife International, 2023). An increase in abundance of the wintering curlew populations was observed all along the East Atlantic flyway (van Roomen et al., 2015), including the so-called Wadden Sea, a part of the North Sea, with a discontinuous series of intertidal flats near the coasts of the Netherlands, Germany, and Denmark (Laursen, 2005; Laursen & Frikke, 2013; Kämpfer & Fartmann, 2022), and the curlew population on the Adriatic coast, and in East Asia (BirdLife International, 2023). An increase in the curlew abundance in the mentioned wintering populations may indirectly evidence of the curlew abundance increase in some of the Russian breeding populations (BirdLife International, 2023). Other possible explanations or contributing factors for the discrepancy between breeding and wintering trends include data limitations and trends being obscured by a climate-mediated shift in the wintering range (Brown, 2015; BirdLife International, 2023). In general, the analysis of the compiled trend data indicates that during the last 15 years the size of the global curlew population declined by 26–34% (Hillis, 2003; Thorup, 2006; Wetland International, 2006; Eaton et al., 2007; BirdLife International, 2023).

Summing up, based on our data and the literature analysis, we suppose that the negative trends in the curlew abundance in the Olonets district in the Republic of Karelia are driven not only by local factors but also by certain global processes, which have caused a decline in some other European populations as well. These birds are likely affected by negative factors on the migration flyways or on wintering sites, although further research is needed to verify this assumption. It is also predicted that climate changes may have a detrimental effect on the curlews during the breeding seasons (Huntley et al., 2007; Renwick et al., 2012; Franks et al., 2017). Wetland area decline caused by climate warming is already considered a reason for a decrease in the abundance of waterfowl and shorebirds (e.g. Delany et al., 2009; Melnikov & Gagina-Scalon, 2014; Krivenko, 2021). The extension of renewable energy sources, such as wind farms, may also affect breeding curlew populations, but more studies are required on this matter as well (Pearce-Higgins et al., 2009). Furthermore, being susceptible to the bird influenza, curlews may be at risk during future outbreaks of the virus (Melville & Shortridge, 2006).

The local-scope factors that should be mentioned as producing a certain negative effect on the curlew abundance are the burning of the last year's herb vegetation, farming intensification, predation, and human disturbance. The first two factors are the most critical, especially herb cover burning, which damages all early nests and undermines the foraging resources available to curlews. The high mortality of eggs and chicks due to intensive agriculture (e.g. Tuellinghoff & Bergmann, 1993; Grant, 1997; Fisher & Walker, 2015), human disturbance (Boschert & Rupp, 1993) and high predation pressure (Berg, 1992; Colhoun et al., 2015; Zielonka et al., 2019) are the main risks in cultivated farmlands and other fragmented landscapes (del Hoyo et al., 1996; Valkama et al., 1999; Douglas et al., 2014). In the Olonets grasslands, curlews are being partially «saved» because they predominantly nest in areas inconvenient for agricultural treatments (e.g. tillage, harvesting), i.e. in the margins, amid rough terrain, near shrub stands. Exactly the loss of such marginal habitats and similar nesting sites, as a consequence of agriculture intensification and enhancement, was one of the main causes of the curlew abundance decline in Europe (Johnsgard, 1981; Baines, 1988; Berg, 1992; del Hoyo et al., 1996; Franks et al., 2017; Douglas et al., 2021). On the other hand, curlews cannot nest in areas put out of the agricultural use due to the fact that land gets rapidly overgrown by tall herbs, shrubs, and forest (Broyer & Roche, 1991; Melnikov, 2017; Sviridova, 2021; BirdLife International, 2023).

According to our data, the season of spring hunting on Anseriformes in the studied part of the Olonets grasslands did not have a significant impact on the curlew abundance. This is partly caused by the fact that our study has been carried out in the «Non-hunting zone», where hunting impact on birds is minimised. In areas, where the spring hunting is being performed, the disturbance factor is possibly more impactful for the birds, and the hunting negatively affects the local bird population in such territories. Spring hunting of curlews is prohibited in Russia. However, in the study area, poachers shoot some of them. Other curlews are undoubtedly under anxiety during the hunting season due to gunshots, vehicle and hunters on nesting sites and hunting-induced massive movements of *Anser* and *Barnacle* species. It is worth noting that hunting has been one of the causes of the abundance decline in some European curlew populations (Johnsgard, 1981). In addition, the natural predators in the Olonets grasslands, capable of ravaging the nests of curlews, are Corvidae, Accipitriformes and Falconiformes, as well as *Vulpes vulpes* (Linnaeus, 1758), *Nyctereutes procyonoides* (J.E. Gray, 1834), and Mustelidae (our data). However, some nests can be ravaged by dogs searching the Olonets grasslands, including the «Non-hunting zone», for wounded game during the hunting season and immediately after this.

The risks listed above are aggravated by the fact that both nests and broods of curlews remain threatened by external negative factors; for instance, eggs are incubated for 26–29 days, and the young chicks can fly only after 5–6 weeks of age (Sviridova, 2021). The high risks over such a long period result in a low reproductive success. Specialists are seriously concerned on a tendency to an increase in frequency of curlew nesting in crop lands, where the breeding success is highly unstable, down to zero (Sviridova et al., 2016). According to various authors (Sviridova et al., 2008; Brown, 2015; Baines et al., 2023), the breeding success in curlews varied depending on years and habitats from 26% to 97%, and in Europe the ratio of the juvenile individuals, starting to fly, per pair of adults varies from 0.27 to 1.05.

The low hatching and chick survival rates in breeding areas are considered the main causes of the decrease in the curlew abundance in 1980–2015, while the survival rate of adult birds is quite high (Brown, 2015). In some regions, the negative influence of the low reproductive success on the total abundance still remains «smoothed down» due to the long life span, typical for the curlew. Gradual ageing of birds in a population with low reproductive success may, however, be resulting in a substantial decline in the nearest future. In many regions of Russia, the abundance of breeding curlews is already now at or below the self-maintenance threshold (Sviridova, 2021). Our predictive assessments of potential future changes in the curlew abundance in the Olonets grasslands suggest that within the next 30–40 years this species is highly likely to become threatened in the study area.

Timely actions are needed to counteract the mentioned threats. Despite the fact that in the «non-hunting zone» we revealed no significant influence of hunting in adjacent areas on birds, as well as of the grassland use intensity, we cannot exclude the possible influence of these factors in the future. It is necessary to conserve curlew breeding habitats, strengthen the protection regime in the Olonets grasslands (preferably through designation of a high-status Protected Areas in the «non-hunting zone»), and widely promote the idea of the curlew conservation and reduce the human disturbance. The currently adopted measures for protecting the migratory bird stopover sites in the Olonets grasslands are insufficient, and they do not match their conservation value and the national and international importance for conservation of European migratory bird populations. To preserve them, proposals for a Protected Area establishment with a special protection regime have been developed (Artemyev et al., 2009, 2022), which can have a positive effect on the abundance of various bird species, including curlews.

Conclusions

Olonets grasslands in the southern Republic of Karelia are an annual breeding and stopover area for the curlew, a Red Data Book species. Its population status has been of global concern since the 1980s. Since 1999 a decline in the curlew abundance has been found in the study area. The results of walking transect surveys showed that over 1999–2023 the total spring abundance of curlews in the Olonets grasslands decreased by 34.4%. The local breeding population of curlews is currently 100–300 pairs, and the abundance of curlews migrating through the Olonets grasslands is 150–2500 birds per year.

Our study has found no evidence that the decline in the curlew abundance depends on the grassland intensity use or bird disturbance during the spring hunting on Anseriformes. On the other hand, the curlew abundance is directly correlated with the local weather conditions, e.g. the curlew density in the Olonets grasslands was lower in warmer spring seasons.

The material collected through the surveys and analysis of the literature suggested that the negative trends in the curlew abundance in the study area are driven not only by local factors but also by some global-scale processes, which cause the abundance decline in other parts of the species range as well. Curlews are probably exposed to negative impacts along flyways or in wintering sites. But additional research is needed to verify this assumption. Other factors presumed to threaten various curlew populations include climate changes, promotion of renewable energy sources, and infections.

In stopovers and breeding areas, the curlew abundance can be affected by burning of last year's herb vegetation, farming intensification, predation, and human disturbance. A long time of both brooding and becoming self-sufficient by juveniles make birds sensitive to these threats. Being considered together, this leads to the low success in curlew reproduction, especially in agrolandscapes. The gradual ageing of birds in a population coupled with a low breeding success may lead to a critical decline in the curlew abundance in the nearest future (Sviridova, 2021). According to our assessments, the curlew abundance in the Olonets grasslands may be decreased to a minimum in the next 30–40 years, estimating this species at the endangered protection category. To counteract these negative predictions, a set of actions is needed to conserve the habitats suitable for curlew breeding, to strengthen the protection regime in the Olonets grasslands (preferably through establishment of high-status Protected Areas), and to promote public awareness of the need to preserve the curlew and reduce its disturbance.

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References

Artemyev A.V., Zimin V.B., Lapshin N.V., Simonov S.A. 2009. Features of the dynamics of spring aggregations of geese (Anseriformes) on the Olonet fields of the Republic of Karelia in 2009. *Russian Journal of Ornithology* 522: 1891–1899. [In Russian]

Artemyev A.V., Lapshin N.V., Khokhlova T.Yu., Matantseva M.V., Simonov S.A. 2016. Main results of ornithological research in Karelia. In: *Role of science in solving the problems of the region and the country: basic and applied research*. Petrozavodsk: Karelian Research Centre of RAS. P. 84–87. [In Russian]

Artemyev A.V., Matanzeva M.V., Simonov S.A. 2019. Taiga Bean Goose (*Anser fabalis fabalis*) on spring stopover site near Olonets, Republic of Karelia, Russia. *Casarca* 21: 81–89. [In Russian]

Artemyev A.V., Lapshin N.V., Simonov S.A., Matantseva M.V., Tolstoguzov A.O. 2020. Long-term trends in abundance of dabbling ducks at the spring migration stopover in the vicinities of Olonets city in the central part of the Republic of Karelia. *Herald of Game Management* 7(1): 31–37. [In Russian]

Artemyev A.V., Khokhlova T.Yu., Yakovleva M.V., Matantseva M.V., Simonov S.A. 2021. New list of Red Data Book birds in the Republic of Karelia. *Russian Journal of Ornithology* 30(2126): 4875–4881. DOI: 10.24412/1026-5627-2021-2126-4875-4881 [In Russian]

Artemyev A.V., Lapshin N.V., Simonov S.A., Matantseva M.V., Tolstoguzov A.O. 2022. Current trends in the dynamics of goose congregations on the Olonets spring migration stopover site (Republic of Karelia, Russia). *Casarca* 24: 15–32. [In Russian]

Baines D. 1988. The effects of improvement of upland, marginal grasslands on the distribution and density of breeding wading birds (Charadriiformes) in northern England. *Biological Conservation* 45(3): 221–236. DOI: 10.1016/0006-3207(88)90141-3

Baines D., Fletcher K., Hesford N., Newborn D., Richardson M. 2023. Lethal predator control on UK moorland is associated with high breeding success of curlew, a globally near-threatened wader. *European Journal of Wildlife Research* 69(1): 6. DOI: 10.1007/s10344-022-01631-5

Balmer D.E., Gillings S., Caffrey B.J., Swann R.L., Downie I.S., Fuller R.J. (Eds.). 2013. *Bird Atlas 2007-11: The Breeding and Wintering Birds of Britain and Ireland*. Thetford: BTO Books Publisher. 720 p.

Berg Å. 1992. Factors affecting nest-site choice and reproductive success of curlews *Numenius arquata* on farmland. *Ibis* 134(1): 44–51. DOI: 10.1111/j.1474-919X.1992.tb07228.x

BirdLife International. 2015. *European Red List of Birds*. Luxembourg: Office for Official Publications of the European Communities. 69 p. DOI: 10.2779/975810

BirdLife International. 2023. *Species factsheet: Numenius arquata*. Available from https://datazone.birdlife.org/species/factsheet/eurasian-curlew-numenius-arquata

Booth Jones K., O'Connell P., Wolsey S., Carrington-Cotton A., Noble D., McCulloch N., Calladine J. 2022. Loss of breeding waders from key lowland grassland sites in Northern Ireland. *Irish Birds* 44: 11–22.

Boschert M., Rupp J. 1993. Brutbiologie des Großen Brachvogels *Numenius arquata* in einem Brutgebiet am südlichen Oberrhein. *Vogelwelt* 5: 199–221.

Broyer J., Roche J. 1991. The nesting population of curlew *Numenius arquata* in the Saone basin. *Alauda* 59: 129–135.

Brown D.J. 2015. International single species action plan for the conservation of the Eurasian curlew *Numenius arquata arquata*, *N. a. orientalis* and *N. a. suschkini*. In: *AEWA Technical Series*. Vol. 58. Bonn, Germany. 68 p.

Butiev V.T. 2001. Eurasian curlew. In: *Red Data Book of the Russian Federation. Animals*. Moscow: Astrel. P. 515–517. [In Russian]

Butiev V.T., Shitikov D.A. 1998. Numbers of Lapwing, curlew and Black-tailed Godwit in Arkhangelsk Region. In: P.S. Tomkovich, E.A. Lebedeva (Eds.): *Breeding waders in Eastern Europe-2000.* Vol. 1. Moscow: Russian Bird Conservation Union. P. 12–17. [In Russian]

Butiev V.T., Shitikov D.A., Lebedeva E.A. 1998. On the numbers of breeding waders in Vologda region. In: P.S. Tomkovich, E.A. Lebedeva (Eds.): *Breeding waders in Eastern Europe-2000.* Vol. 1. Moscow: Russian Bird Conservation Union. P. 18–23. [In Russian]

Bykov Yu.A., Romanov V.V., Sergeev M.A. 2018. Eurasian curlew. In: *Red Data Book of the Vladimir Region*. Tambov: Tambov Printing Union. P. 361. [In Russian]

Colhoun K., Mawhinney K., Peach W.J. 2015. Population estimates and changes in abundance of breeding waders in Northern Ireland up to 2013. *Bird Study* 62(3): 394–403. DOI: 10.1080/00063657.2015.1058746

Delany S., Scott D., Dodman T., Stroud D. 2009. *An atlas of wader populations in Africa and Western Europe*. Wageningen: Wetlands International. 524 p.

del Hoyo J., Elliott A., Sargatal J. (Eds.). 1996. *Handbook of the Birds of the World*. Vol. 3: Hoatzin to Auks. Barcelona: Lynx Edicions. 821 p.

Douglas D.J.T. 2020. Eurasian curlew *Numenius arquata*. In: *European Breeding Bird Atlas*. Vol. 2: Distribution, Abundance and Change. Barcelona: European Bird Census Council & Lynx Edicions. P. 314–315.

Douglas D.J.T., Bellamy P.E., Stephen L.S., Pearce-Higgins J.W., Wilson J.D., Grant M.C. 2014. Upland land use predicts population decline in a globally near-threatened wader. *Journal of Applied Ecology* 51(1): 194–203. DOI: 10.1111/1365-2664.12167

Douglas D.J.T., Lewis M., Thatey Z., Teuten E. 2021. Wetlands support higher breeding wader densities than farmed habitats within a nature-rich farming system. *Bird Study* 68(1): 100–111. DOI: 10.1080/00063657.2021.1970104

Eaton M.A., Austin G.E., Banks A.N., Conway G., Douse A., Grice P.V., Hearn R.D., Hilton G.M., Hoccom D., Musgrove A.J., Noble D.G.N., Ratcliffe N., Rehrisch M.M., Worden J., Wotton S. 2007. *The state of the UK's birds 2006*. Sandy, Bedfordshire: RSPB, BTO, WWT, CCW, EHS, NE, SNH. 40 p.

Elts J., Leito A., Leivits A., Luigujõe L., Mägi E., Nellis R., Nellis R., Ots M., Pehlak H. 2013. Status and numbers of Estonian birds, 2008−2012. *Hirundo* 26(2): 80–112.

Fisher G., Walker M. 2015. Habitat restoration for curlew *Numenius arquata* at the Lake Vyrnwy reserve, Wales. *Conservation Evidence* 12: 48–52.

Franks S.E., Douglas D.J.T., Gillings S., Pearce-Higgins J.W. 2017. Environmental correlates of breeding abundance and population change of Eurasian curlew *Numenius arquata* in Britain. *Bird Study* 64(3): 393–409. DOI: 10.1080/00063657.2017.1359233

Galchenkov Yu.D. 2017. Eurasian curlew *Numenius arquata* Linnaeus, 1758. In: *Red Data Book of the Kaluga Region.* Vol. 2: Animal World. Kaluga: Vash Dom. P. 294–295. [In Russian]

Golovan V.I., Khrabry V.M. 2018. Eurasian curlew *Numenius arquata* (Linnaeus, 1758). In: *Red Data Book of the Leningrad Region. Animals*. Saint Petersburg: Papirus. P. 426–427. [In Russian]

Gorelick N., Hancher M., Dixon M., Ilyushchenko S., Thau D., Moore R. 2017. Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment* 202: 18–27. DOI: 10.1016/j.rse.2017.06.031

Grant M.C. 1997. Breeding curlew in the UK: RSPB research and implications for conservation. *RSPB Conservation Review* 11: 67–73.

Harris S.J., Massimino D., Newson S.E., Eaton M.A., Balmer D.E., Noble D.G., Musgrove A.J., Gillings S., Procter D., Pearce-Higgins J.W. 2014. *The Breeding Bird Survey 2014*. BTO Research Report 673. Thetford: British Trust for Ornithology. 22 p.

Hayhow D.B., Conway G., Eaton M.A., Grice P.V., Hall C., Holt C.A., Kuepfer A., Noble D.G., Oppel S., Risely K., Stringer C., Stroud D.A., Wilkinson N., Wotton S. 2014. *The State of the UK's Birds 2014*.

Sandy, Bedfordshire: RSPB, BTO, WWT, JNCC, NE, NIEA, NRW, SNH. 54 p.

Hillis J.P. 2003. Rare Irish breeding birds, 1992–2001. *Irish Birds* 7(2): 157–172.

Hötker H., Jeromin H., Melter J. 2007. Entwicklung der Brutbestände der Wiesen-Limikolen in Deutschland – Ergebnisse eines neuen Ansatzes im Monitoring mittelhäufiger Brutvogelarten. *Vogelwelt* 128: 49–65.

Huntley B., Green R.E., Collingham Y.C., Willis S.G. 2007. *A climatic atlas of European breeding birds*. Durham & Sandy, U.K. and Barcelona, Spain: Durham University, RSPB & Lynx Edicions. 528 p.

Ivanchev V.P. 2011. Eurasian curlew. In: *Red Data Book of the Ryazan Region.* 2nd edition, updated and revised. Ryazan: Golos Provintsii. P. 100. [In Russian]

Johnsgard P.A. 1981. *The plovers, sandpipers and snipes of the world*. Lincoln: University of Nebraska. 519 p.

Kämpfer S., Fartmann T. 2022. Natural coastal dunes on Wadden Sea islands as a refuge for an endangered wader species. *Journal of Coastal Conservation* 26(6): 53. DOI: 10.1007/s11852-022-00897-w

Khokhlova T.Y., Artemiev A.V., Yakovleva M.V. 2023. Waders in the Red Book of the Republic of Karelia. *Environmental Protection and Preservation* 1: 123–129. [In Russian]

Komsta L. 2022. *Outliers: Tests for Outliers*. R package version 0.15. Available from https://CRAN.R-project.org/package=outliers

Krivenko V.G. 2021. Global climate warming from the position of the Cosmogenic theory of dynamics of areas and animals in the Northern Hemisphere. *Bulletin of the Russian Academy of Natural Sciences* 21(3): 96–106. [In Russian]

Lappo E., Tomkovich P.S., Syroechkovskiy E.E. 2014. *Atlas of Breading Waders in the Russian Arctic.* Moscow: VACO. 448 p. [In Russian]

Lehtonen L. 1943. Piirteitä Pohjois – ja Keski-Vienan linnustosta. *Ornis Fennica* 20(2–3): 33–58.

Lapshin N.V., Zimin V.B., Artemyev A.V., Simonov S.A. 2012. Charadriidae birds of the Olonets spring aggregations (Karelia). In: *Modern problems of nature management, hunting and fur farming*. Vol. 1. Kirov. P. 219–220. [In Russian]

Laursen K. 2005. Curlews in the Wadden Sea – effects of shooting protection in Denmark. *Wadden Sea Ecosystem* 20: 171–184.

Laursen K., Frikke J. 2013. Rastende vandfugle i Vadehavet 1980–2010. *Dansk Ornitologisk Forenings Tidsskrift* 107(1): 1–184.

Mei W., Yu G. 2020. *BasicTrendline: Add Trendline and Confidence Interval of Basic Regression Models to Plot*. R package version 2.0.5. Available from https://CRAN.R-project.org/package=basicTrendline

Melnikov V.N. 2017. Curlew. In: *Red Data Book of the Ivanovo Region*. Vol. 1: Animals. 2nd ed. Ivanovo: Nauchnyi Konsultant. P. 177. [In Russian]

Melnikov Yu.I., Gagina-Scalon T.N. 2014. Changes in bird fauna of Lake Baikal throughout the XX and the beginning of XXI centuries. *Amurian Zoological Journal* 6(4): 418–437. [In Russian]

Melville D.S., Shortridge K.F. 2006. Migratory waterbirds and avian influenza in the East Asian-Australasian Flyway with particular reference to the 2003–2004 H5N1 outbreak. In: G. Boere, C. Galbraith, D. Stroud (Eds.): *Waterbirds Around the World.* Edinburgh: The Stationery Office. P. 432–438.

Mishchenko A.L., Belik V.P., Borodin O.V., Sarychev S.V., Sukhanova O.V., Krasnov Yu.V., Preobrazhenskaya E.S., Malovichko L.V., Shepel A.I., Yakovleva M.V., Morozov V.V., Volkov S.V., Sharikov A.V., Grishanov V.G., Rykova S.Yu., Yakovlev A.A., Spiridonov S.N., Lapshin A.S., Rakhimov I.I., Moskvichev A.N., Karyakin I.V., Piskunov V.V., Antonchikov A.N., Murav'ev I.V., Korkina S.A., Frolov V.V. 2017. *Estimation of abundance and dynamics for birds of the European part of Russia (results of the European Red List of Birds project)*. Moscow: BirdsRussia. 63 p. [In Russian]

Neifeldt I.A. 1958. On the avifauna of southern Karelia. *Proceedings of Zoological Institute of the Academy of Sciences of the USSR* 25: 183–254. [In Russian]

Noskov G.A., Rymkevich T.A., Kovalev D.N. 2016. Eurasian curlew *Numenius arquata*. In: G.A. Noskova, T.A. Rymkevich, A.R. Gaginskaya (Eds.): *Migration of Birds of Northwest Russia. Non-passerines*. Saint Petersburg: Professional. P. 418–423.

Pearce-Higgins J.W., Langston R.H.W., Bainbridge I.P., Bullman R. 2009. The distribution of breeding birds around upland wind farms. *Journal of Applied Ecology* 46(6): 1323–1331. DOI: 10.1111/j.1365-2664.2009.01715.x

QGIS.org. 2022. *QGIS Geographic Information System*. Open Source Geospatial Foundation Project. Available from https://qgis.org

R Core Team. 2021. *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available from https://www.R-project.org

Red Data Book of the Republic of Karelia. Belgorod: Konstanta, 2020. 448 p.

Renwick A.R., Massimino D., Newson S.E., Chamberlain D.E., Pearce-Higgins J.W., Johnston A. 2012. Modelling changes in species' abundance in response to projected climate change. *Diversity and Distributions* 18(2): 121–132. DOI: 10.1111/j.1472-4642.2011.00827.x

Rigal S., Dakos V., Alonso H., Auniņš A., Benkő Z., Brotons L., Chodkiewicz T., Chylarecki P., de Carli E., del Moral J.C., Domşa C., Escandell V., Fontaine B., Foppen R., Gregory R., Harris S., Herrando S., Husby M., Ieronymidou C., Jiguet F., Kennedy J., Klvaňová A., Kmecl P., Kuczyński L., Kurlavičius

P., Kålås J.A., Lehikoinen A., Lindström Å., Lorrillière R., Moshøj C. et al. 2023. Farmland practices are driving bird population decline across Europe. *Proceedings of the National Academy of Sciences of the United States of America* 120(21): e2216573120. DOI: 10.1073/pnas.2216573120

RStudio Builds. 2021. *Ghost Orchid*. Version 2021.09.1+372.pro1. Available from https://dailies.rstudio.com/version/2021.09.1+372/

Sviridova T.V. 2014. Status of rare species of waders in the Non-Chernozem Center of Russia at the turn of the 20th and 21st centuries. In: *Rare bird species of the Non-Chernozem Center of Russia*. Moscow: Moscow State University. P. 65–91. [In Russian]

Sviridova T.V. 2019. Distribution and abundance of rare nesting waders in the Non-Chernozem center of Russia at the beginning of the 21st century. In: *Rare bird species of the Non-Chernozem Center of Russia*. Moscow: Moscow State University. P. 30–71. [In Russian]

Sviridova T.V. 2020. Eurasian curlew *Numenius arquata*. In: M.V. Kalyakin, O.V. Voltzit (Eds.): *Atlas of nesting birds of the European part of Russia*. Moscow: Fiton XXI. P. 352–355. [In Russian]

Sviridova T.V. 2021. Curlew *Numenius arquata* (Linnaeus, 1758). In: *Red Data Book of the Russian Federation. Animals*. Moscow: VNII Ecologiya. P. 745–747. [In Russian]

Sviridova T.V., Volkov S.V., Koltsov D.B., Konovalova T.V., Zubakin V.A. 2008. Dynamics of spatial distribution, abundance and breeding success of the Eurasion curlew in the north of the Moscow region under the influence of anthropogenic factors and weather. *Bulletin of Moscow Society of Naturalists* 113(1): 12–20. [In Russian]

Sviridova T.V., Koltsov D.B., Grinchenko O.S., Volkov S.V. 2016. Waders in the conditions of ecological and agricultural management, recession and revival of agriculture in the Moscow region. In: *Issues of ecology, migration and protection of waders of Northern Eurasia*. Ivanovo. P. 327–334. [In Russian]

Thorup O. 2006. *Breeding waders in Europe 2000*. Thetford: International Wader Study Group. 142 p.

Tomkovich P.S., Lebedeva E.A. (Eds.). 1998. *Breeding Waders of Eastern Europe-2000*. Vol. 1. Moscow: Union for the Protection of Birds of Russia Publ. 123 p. [In Russian]

Tomkovich P.S., Lebedeva E.A. (Eds.). 1999. *Breeding Waders of Eastern Europe-2000.* Vol. 2. Moscow: Union for the Protection of Birds of Russia Publ. 106 p. [In Russian]

Tuellinghoff R., Bergmann H. 1993. Curlew habitats in Lower Saxony: preferred and avoided structures in the agricultural landscape. *Vogelwarte* 37: 1–11.

Tyulkin Yu.A. 2012. Eurasian curlew. In: *Red Data Book of the Udmurt Republic.* 2nd ed. Cheboksary: Perfektum. P. 139. [In Russian]

Tyulkin Yu.A. 2020. Eurasian curlew *Numenius arquata* (Linnaeus, 1758). In: *Red Data Book of the Tyumen Region*. Kemerovo: TEKHNOPRINT. P. 74. [In Russian]

Valkama J., Currie D., Korpimäki E. 1999. Differences in the intensity of nest predation in the curlew *Numenius arquata*: A consequence of land use and predator densities?. *Ecoscience* 6(4): 497–504. DOI: 10.1080/11956860.1999.11682552

van Roomen M., Nagy S., Foppen R., Dodman T., Citegetse G., Ndiaye A. 2015. *Status of coastal waterbird populations in the East Atlantic Flyway. With special attention to flyway populations making use of the Wadden Sea*. Programme Rich Wadden Sea. Leeuwarden, the Netherlands, Sovon, Nijmegen, Wageningen, BirdLife International, Cambridge, United Kingdom, Common Wadden Sea Secretariat, Wilhelmshaven, Germany. 79 p.

Wetland International. 2006. Relict Gull surveys in Hongjianao, Shaanxi Province. *Newsletter of China Ornithological Society* 15(2): 29.

Zielonka N.B., Hawkes R.W., Jones H., Burnside R.J., Dolman P.M. 2019. Placement, survival and predator identity of Eurasian curlew *Numenius arquata* nests on lowland grass-heath. *Bird Study* 66(4): 471–483. DOI: 10.1080/00063657.2020.1725421

Zimin V.B., Ivanter E.V. 1974. *Birds*. Petrozavodsk: Karelia Publisher. 256 p. [In Russian]

Zimin V.B., Sazonov S.V., Lapshin N.V., Khokhlova T.Yu., Artemyev A.V., Annenkov V.G., Yakovleva M.V. 1993. *Avifauna of Karelia*. Petrozavodsk: Petrozavodsk: Karelian Research Centre of RAS. 220 p. [In Russian]

Zimin V.B., Sazonov S.V., Artemyev A.V., Lapshin N.V., Khokhlova T.Yu. 1998. The avifauna of protected areas and areas perspective for protection in the border zone of the Republic of Karelia. In: *Biodiversity inventories and studies in the areas of the Republic of Karelia bordering on Finland*. Petrozavodsk: Karelian Research Centre of RAS. P. 116–131. [In Russian]

Zimin V.B., Artemyev A.V., Lapshin N.V., Tyulin A.R. 2007. *Olonets spring gatherings of birds. General characteristics. Geese.* Moscow: Nauka. 299 p. [In Russian]

Zimin V.B., Artemyev A.V., Lapshin N.V. 2009. KOTR European Russia: Olonets Plain – KA-005. Available from http://www.rbcu.ru/kotr/ka005.php [In Russian]

ДИНАМИКА ЧИСЛЕННОСТИ *NUMENIUS ARQUATA* (CHARADRIIFORMES, AVES) В АГРОЛАНДШАФТАХ ЮЖНОЙ КАРЕЛИИ (СЕВЕРО-ЗАПАД РОССИИ)

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Олонецкие поля (61.041111° N, 32.931389° E) являются крупнейшими агроландшафтами Республики Карелия (северо-запад России), одним из мест наиболее массовой концентрации птиц на весенних миграционных стоянках в Северной Европе и местом гнездования видов, связанных с сельскохозяйственными угодьями. Эта территория играет важную роль в жизни птиц многих видов и включена в список Ключевых орнитологических территорий России международного значения. Однако уровень ее охраны невысок – на части Олонецких полей (49 км^2) с 1993 г. запрещена лишь весенняя охота. Поэтому необходимо повышение природоохранного статуса этой территории и мер защиты птиц, а также ведение мониторинга численности охраняемых и уязвимых видов, использующих ее на разных этапах годового цикла. Одним из таких видов является *Numenius arquata* (далее – кроншнеп), вид с сокращающейся численностью и распространением многих популяций. Этот вид использует Олонецкие поля как для остановки на весенней миграции, так и для гнездования. Мы проанализировали данные регистраций кроншнепов на Олонецких полях, полученных в апреле – мае в 1999–2023 гг. методами пеших и автомобильных маршрутных учетов. Эти данные мы сопоставили с данными по температуре воздуха и по уровню хозяйственной эксплуатации полей, а также проанализировали временную зависимость весенней численности кроншнепов от даты и от года наблюдений. Рабочая гипотеза заключалась в предположении, что численность кроншнепов снижается в сезоны с холодными веснами, в сезоны с интенсивной эксплуатации полей, а также с течением времени. Последнее предположение связано с отмеченным в минувшие десятилетия сокращением численности кроншнепов в разных местах видового ареала. Собранные данные показали постоянное присутствие особей этого вида на Олонецких полях в апреле – мае. Отмечено, что в период миграции кроншнепы равномерно использовали участки полей, в целом пригодные для их гнездования и остановок, не отдавая явного предпочтения каким-либо зонам. Однако в качестве мест гнездования они выбирали участки, наиболее неудобные для сельскохозяйственной обработки. По-видимому, равномерное распределение кроншнепов по полям было преимущественно обусловлено особями, кормящимися на миграционных остановках. Величина части местной популяции, гнездящейся в обследуемой зоне Олонецких полей (49 км^2), в 1999–2023 гг. изменялась от 30 до 150 пар. При этом в 2019–2023 гг. она составляла 30–90 пар. Гнездящаяся группировка кроншнепов на всех Олонецких полях (180 км^2) в 1999–2023 гг. насчитывала 100–1200 пар в разные сезоны. При этом в 2019–2023 гг. ее величина не превышала 100–300 пар. На миграции в обследуемой части Олонецких полей ежегодно останавливалось 90–750 особей кроншнепа, а на всех Олонецких полях в целом – 150–2500 особей. На настоящий момент не было выявлено зависимости общей численности кроншнепов в районе исследований от интенсивности эксплуатации полей, что, видимо, связано с сохранением мест, пригодных для миграционной остановки и гнездования. В свою очередь, было отмечено снижение численности кроншнепов в весенние сезоны с более теплой погодой. По-видимому, в такие сезоны часть кроншнепов улетает дальше на север. В более холодные сезоны больше птиц оседают на этих полях или задерживаются на них на трассе миграции. В многолетнем аспекте, за 25-летний период, было зарегистрировано снижение на 34.4% общей численности кроншнепов, регистрируемых на Олонецких полях. Видимо, негативная динамика численности кроншнепа на территории исследования была обусловлена не только местными факторами, но и глобальными процессами, вызывающими сокращение численности изученной и ряда других европейских популяций. Вероятно, эти птицы сталкиваются с определенными проблемами на путях миграции или зимовок, но это предположение требует проведения дальнейших исследований. Среди факторов местного значения, потенциально способных оказать негативное влияние на численность кроншнепов, следует назвать выжигание прошлогодней травы, интенсификацию сельскохозяйственных работ, хищничество и беспокойство птиц человеком. Наши результаты прогнозирования возможностей дальнейшего изменения численности у кроншнепов на Олонецких полях свидетельствуют о том, что в течение 30–40 лет изучаемый вид здесь с высокой вероятностью может перейти в разряд «исчезающие». Для предотвращения этого необходимо сохранять места, в которых кроншнепы могут гнездиться, усилить режим охраны полей (желательно с созданием особо охраняемых природных территорий высокого статуса) и проводить среди населения пропаганду охраны кроншнепа и снижения степени его антропогенного беспокойства.

Ключевые слова: агроландшафт, мониторинг, особо охраняемая природная территория, охраняемый вид, кулик

DISTRIBUTION MODELLING OF THE CAUCASIAN ENDEMIC *FRITILLARIA LATIFOLIA* AGAINST THE BACKGROUND OF CLIMATE CHANGE

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Current climate change, habitat degradation, pastoralism, shoot and bulb harvesting pose serious threats to the rare Caucasian endemic *Fritillaria latifolia* throughout its range. Knowledge of the limiting factors, species range dynamics in relation to climate change and the role of Protected Areas in species distribution are necessary to develop an effective conservation system at present and in the future. This was aimed (1) to determine the most suitable set of abiotic predictors for modelling *Fritillaria latifolia* localisation, (2) to formalise environmental and anthropogenic factors in species distribution models, (3) to predict the possible changes in the species range in relation to climatic changes, (4) to identify refugia with a consistently high probability of the species occurrence despite climatic changes. We applied Maxent software for species habitat modelling to build current and climatic models of the *Fritillaria latifolia* distribution, considering the abiotic variables and anthropogenic predictors such as the distance to Protected Areas and grasslands. Distances to anthropogenic infrastructure were calculated with the Path Distance measure considering the horizontal straight-line distance, surface distance and vertical factor. We also formalised the area accessibility (movement factor) through the distance to optimal sites (plots with 0.8 threshold of habitat suitability), where the probability of species occurrence was higher than 0.5. The most important abiotic variables in the species distribution were the Emberger's pluviothermic quotient, with optimal values corresponding to humid and perhumid climates, and the terrain roughness index, with optimal values ranging from nearly level (81–116) to intermediately rugged (162–239) slopes. Distance to Protected Areas (0–1 km) was the third important predictor of the *Fritillaria latifolia* current distribution, while the distance to grasslands contributed less to the model. The distance of suitable areas from optimal habitats (area accessibility) was 15 km. The species current core ranges are localised in the Western and Central Caucasus, Western and Central Transcaucasia, and the northwestern ridges of the Lesser Caucasus within a network of Protected Areas covering most of the highlands. The optimistic socio-economic pathway SSP1-2.6 predicted a 1.6-fold decrease in the area of species optimal habitats from 2021 to 2100. The pessimistic SSP5-8.5 scenario predicted 122-fold habitat area reduction. According to SSP1-2.6 climatic models, by 2100 the refugia area would be 172.4 km^2 in the highlands of the western and central parts of the Greater Caucasus, including the Caucasus State Nature Reserve and Teberda National Park. These areas should be prioritised for the conservation of *Fritillaria latifolia* populations.

Key words: Biotic-Abiotic-Movement concept, Maxent, Protected Area, refugia, socio-economic pathways

Introduction

Current climate change poses a serious threat to the global biodiversity (Banag et al., 2015; Mazangi et al., 2016) and reduces the effectiveness of local and regional conservation and management strategies (Van Dyke, 2008). Climate change is a pressing issue for the Caucasus Mountains, where the average annual air temperature increased by 0.2–0.4°C between the 1960s and 2010 (Atayev & Bratkov, 2014). Biodiversity of mountain ecosystems is particularly sensitive to climate change (Guerrina et al., 2016). Endemic species, with their localised populations and low dispersal rates, are considered among the most vulnerable components of the mountain flora (Van Dyke, 2008; Banag et al., 2015; Guerrina et al., 2016; Christmas et al., 2016). One of the rare Caucasian endemics is *Fritillaria latifolia* Willd. It is native to the mountain meadow ecosystems of the ecoregion. Despite a number of population-based studies (e.g. Thazaplizheva & Chadaeva, 2012; Tania & Abramova, 2013; Yamalov et al., 2014; Pshegusov et al., 2019), the current knowledge about the factors limiting *Fritillaria latifolia* distribution remains extremely scarce. Information on the species range dynamics in relation to climate change and the role of Protected Areas in its predicted distribution is also still lacking. However, knowledge of the distribution predictors and location of refugia is necessary to develop an effective conservation system for *Fritillaria latifolia* at present and in the future.

The issue can be addressed through Species Distribution Models (SDMs). Based on the statistical processing of geographic species records and layers of topographic and climate information, SDM is considered an efficient method for studying the species potential distribution (Elith et al., 2006; Peterson et al., 2011; Duarte et al., 2019; Bowen & Stevens, 2020; Sillero et al., 2021). This is particularly useful in mountainous areas with complex, inaccessible basin-and-range terrain. Within «bioclimate envelope» modelling, SDMs typically include only abiotic environmental predictors of the species distribution. At the same time, interspecific interactions, as well as the widespread impact of human activity, represent integral components of species ecological niches and influence species distribution. Accounting for biotic and anthropogenic factors in the models remains a relevant methodological challenge in SDM. Our study therefore is focused on the Biotic-Abiotic-Movement (BAM) concept, which integrates three key sets of factors (namely B-factors (biotic predictors including anthropogenic factors in this study), A-factors (abiotic environmental variables), and M-factors (movement, dispersal capability or area accessibility)) into single-species models (Soberón & Peterson, 2005; Peterson, 2006; Peterson et al., 2011; Peterson & Soberón, 2012). This concept allows an analysis of the «occupied distributional area», which corresponds most closely to the actual species distribution (Soberón & Peterson, 2005; Peterson & Soberón, 2012).

In this context, this study was aimed to investigate the abiotic and anthropogenic factors, and area accessibility, which could affect the distribution of *Fritillaria latifolia* in the Caucasus. This knowledge is important, as it can form the basis for an effective system of species preservation. The research objectives were (1) determining the most suitable set of abiotic predictors for modelling the species localisation, (2) formalising environmental and anthropogenic factors in SDMs, (3) predicting the possible changes in the species range in relation to climatic changes, and (4) identifying refugia with a consistently high probability of the species occurrence despite climatic changes. We hypothesised that the distance to Protected Areas is one of the key factors in the species distribution at present and in the future.

Material and Methods

Target species and study area

Fritillaria latifolia is a striking, well recognised bulbous geophyte species distributed in mountain grasslands of the Ciscaucasia, the North Caucasus, Western and Eastern Transcaucasia (Tania & Abramova, 2013; Batsatsashvili et al., 2017; Pshegusov et al., 2019). The species belongs to the psychrophytes, which prefer cold and wet habitats (Red Data Book of the Chechen Republic, 2020). As a hydrophilic species (Yamalov et al., 2014; Batsatsashvili et al., 2017), it occurs mainly on gentle river terraces (Tania & Abramova, 2013) and couloirs with long-lasting snow cover (Pshegusov et al., 2019) in subalpine and alpine wet and marshy meadows, often on peaty soils (Yamalov et al., 2014; Batsatsashvili et al., 2017). The decline in populations of this Caucasian endemic throughout its range is caused by pastoralism, habitat degradation, and shoot and bulb harvesting (Tania & Abramova, 2013; Pshegusov et al., 2019). This species has been classified as «Rare species» in the Red Data Book of the Republic of Kabardino-Balkaria (2018) and the Red Data Book of the Chechen Republic (2020).

The Caucasus ecoregion (about 390 000 km^2 between 38–47° N and 36–50° E) was considered the study area. It comprises several climate-orographic parts, namely the Ciscaucasia, the North Caucasus and Transcaucasia (parts of the Greater Caucasus), the Colchis and Kura-Araks Lowlands, the Lesser Caucasus, and the Transcaucasian Highland (Fig. 1a).

The Caucasus ecoregion includes the territories of the Russian Federation, Azerbaijan, Georgia, and Armenia. The Ciscaucasia is dominated by a warm continental climate (Dfa according to the Köppen-Geiger classification) (Fig. 1b). The prevailing climate of the Greater Caucasus is warm summer continental (Dfb) in the middle mountains and cool summer continental (Dfc) or alpine (ET) in the highlands. The North-Western Caucasus and Western Transcaucasia have a predominantly humid subtropical (Cfa) and oceanic (Cfb) climate. Aridity of the climate increases towards the southeast of the Greater Caucasus. A humid subtropical and oceanic climate also prevails in the Colchis Lowland and the northwestern part of the Kura-Araks Lowland. In the southeastern part of the Kura-Araks Lowland, the climate is cold semi-arid (BSk). The mountainous areas of the Lesser Caucasus and Transcaucasian Highland have a warm summer continental climate with increasing aridity towards the southeast. In the southern part of the Transcaucasian Highland, a cold semi-arid climate prevails. The main tree species in the foothills and middle mountains of the Caucasus are *Fagus orientalis* Lipsky, *Carpinus betulus* L. and *Quercus* spp. *Pinus sylvestris* L. and *Betula* spp. are widespread in the middle mountains and highlands. *Picea orientalis* (L.) Peterm. and *Abies nordmanniana* (Steven) Spach occur in the North-Western Caucasus and Western Transcaucasia, while *Juniperus* spp. are common mainly in the Transcaucasian Highland and Lesser Caucasus. The plains, foothills and lowlands of the Caucasus ecoregion are mainly used for agriculture. Subalpine and alpine grasslands historically serve as grasslands.

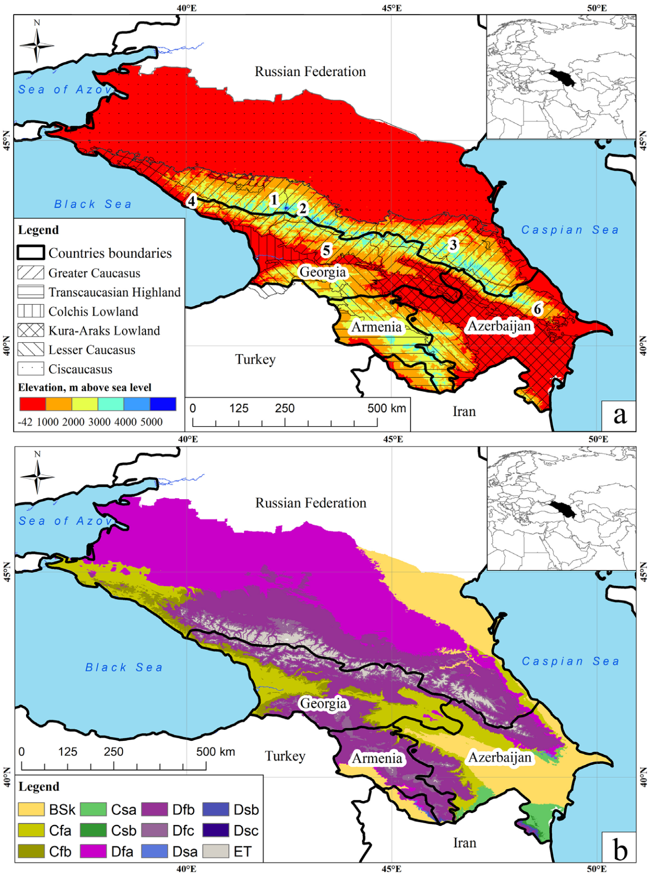

Fig. 1. The geographic location, orography (a) and climate classification scheme (b) of the study area. The climate classification scheme was built based on monthly mean temperature and precipitation data from WorldClim2 using the Saga Gis v. 7.8.2 algorithm of Conrad et al. (2015). Köppen-Geiger climate classification and colour scheme were sourced from Peel et al. (2007). Designations: 1 – Western Caucasus, 2 – Central Caucasus, 3 – Eastern Caucasus (parts of the North Caucasus), 4 – Western Transcaucasia, 5 – Central Transcaucasia, 6 – Eastern Transcaucasia; BSk – cold semi-arid climate, Cfa – humid subtropical climate, Cfb – oceanic climate, Csa – Mediterranean hot summer climate, Csb – Mediterranean warm or cool summer climate, Dfa, Dfb and Dfc – hot, warm and cool summer continental climate respectively, Dsa, Dsb and Dsc – hot, warm and cool dry summer continental climate respectively, ET – alpine climate.

Geographic records and environmental variables

The study design, including assessment and manipulation of spatial data (presence points, environmental layers), model development and evaluation, was summarised in Electronic Supplement 1. We used 57 geographic records of *Fritillaria latifolia* from the 2013–2022 expedition surveys and 82 occurrence data from the Global Biodiversity Information Facility (GBIF.org, 2023). To address the problem of spatial clustering of presence points, we applied spatial thinning as one of the popular correction methods (Petrosyan et al., 2020) (Electronic Supplement 1). Based on the removal of geographic records, spatial thinning produces an occurrence dataset, from which efficient SDM models are constructed (Kramer-Schadt et al., 2013; Syfert et al., 2013; Aiello-Lammens et al., 2015; Sillero et al., 2021). Accordingly, geographic records were checked for duplicates and sparse to one data per 1 km^2 grid cell. As a result, 122 presence points remained after the spatial thinning. Then, the dataset was tested for spatial clustering using the Average Nearest Neighbour Index (Clark & Evans, 1954), which revealed a clustered distribution of 122 presence points (Electronic Supplement 2: Table S1, Fig. S1). When re-thinning over a distance of 14 km, 113 randomly distributed presence points remained (Electronic Supplement 2: Table S1, Fig. S1). The R packages (R Core Team, 2023) used for spatial thinning and testing for spatial clustering were specified in Electronic Supplement 3.

To determine the most suitable abiotic predictors for modelling *Fritillaria latifolia* localisations (Electronic Supplement 1), we used two sets of environmental variables for comparative predictor analysis: 1) WorldClim2 bioclimatic parameters (Fick & Hijmans, 2017; WorldClim2, 2023) and GMTED2010 topographic data (Danielson & Gesch, 2011; GMTED2010, 2023); 2) ENVIREM (ENVIronmental Rasters for Ecological Modeling) climatic and topographic variables (Title & Bemmels, 2018; ENVIREM, 2023). To select uncorrelated environmental layers, we applied the VIF (Variance Inflation Factor) test in R (VIF threshold ≤ 3) (Electronic Supplement 1). As a result, five ENVIREM variables and eight WorldClim2+GMTED2010 predictors were involved in the analysis (Electronic Supplement 2: Table S3).

To check, whether sampling bias is a problem (Kramer-Schadt et al., 2013; Merow et al., 2013; Sillero et al., 2021), we compared the distribution of predictor values for both ENVIREM and

WorldClim2+GMTED2010 datasets (Electronic Supplement 1). According to Mann-Whitney U-test for two independent samples, the distributions of predictor values were similar only in the pair of presence points and background points for the ENVIREM set, indicating the absence of bias (Electronic Supplement 2: Table S2). High similarity was also identified when comparing biased and unbiased ENVIREM A-models using the agreement coefficient (Ji & Gallo, 2006; Riemann et al., 2010) and Pearson correlation coefficient r (Electronic Supplement 2). Thus, no sampling bias problem was revealed when using 113 occurrence points (obtained after spatial thinning), background biased points and ENVIREM dataset. Therefore, already at this stage of the study, the ENVIREM A-model was prioritised for further analysis.

In this study, we considered anthropogenic factors as a part of the biotic predictors of the species distribution. Given the susceptibility of *Fritillaria latifolia* populations to overgrazing and direct human destruction, we used the distances to grasslands and Protected Areas as the main anthropogenic factors. Estimating distances from target species to anthropogenic infrastructure is a common method of accounting for human activity in SDMs (Ortiz-Urbina et al., 2020; Vignali et al., 2021; Sharma et al., 2023). However, Euclidean distance, as the most popular tool in this process, is obviously not suitable for studying mountainous areas, as it does not consider the altitude gradient. Therefore, we used the Path Distance measure (path_landuse and path_PAs) calculated with horizontal straight-line distance, surface distance and vertical factor (McCoy et al., 2001). Path Distance was estimated for each grid cell as the distance to the nearest object, considering altitude gradient (McCoy et al., 2001). The input data were represented by a spatial feature class from the NextGIS vector map sets (NextGIS, 2023) and the digital altitude model GMTED2010 (Amatulli et al., 2018).

The area accessibility (movement factor) is an important concept in SDM, irrespective of the algorithm used (Soberón & Osorio-Olvera, 2023). Our approach to formalising the movement factor was to represent area accessibility through the distance to optimal sites (plots with 0.8 threshold of habitat suitability), on which the probability of species occurrence was higher than 0.5 (Pshegusov et al., 2022).

BAM concept allows the effects of the three factors to be studied separately by building A-, BA- and BAM-models. In the A-models, we used the abiotic variables selected by the VIF test. In the BA-models, we considered the abiotic variables and anthropogenic predictors (VIF ≤ 3) such as the distance to grasslands (path_landuse) and Protected Areas (path_PAs). The raster of distances to optimal areas (sites with 0.8–1.0 probability of species occurrence), where the probability of *Fritillaria latifolia* occurrence remained above 0.5, was used as a movement-layer in the BAM-model. The resolution of the resulting layers was 1 km per pixel.

Model development and evaluation

The modelling procedures were described in ODMAP protocol (Electronic Supplement 4). The R packages used for model development and evaluation were specified in Electronic Supplement 3.

In this study, we applied Maxent v. 3.4.3 (Phillips et al., 2017) for species habitat modelling. It is considered one of the most robust and efficient modelling methods based on presence-only data (Elith et al., 2006; Phillips & Dudík, 2008), especially when rare species with a small sample size are involved (Elith et al., 2011; Qin et al., 2017; Vignali et al., 2021). Identification of the optimal set of Maxent model parameters was shown in Overview/SDM algorithms/Model complexity of the ODMAP protocol (Electronic Supplement 4). Selection of optimal model settings was also shown in Overview/SDM algorithms/Selection of optimal models in the ODMAP protocol (Electronic Supplement 4).

We calculated the percentage contribution of predictors (Phillips et al., 2017) to assess their importance in Maxent models. The optimal variable values were obtained from the response curves by cutting off at a threshold of 0.8. Different thresholds are used to convert continuous probabilities calculated in Maxent into discrete presence/absence predictions (Liu et al., 2013), and there is no uniform method for defining the habitat suitability threshold (Glover-Kapfer, 2015). To reduce the risk of misidentification, it is advisable to choose a high threshold for habitats with a high degree of suitability (Pearson et al., 2004). In this study we used a fixed high threshold of 0.8 for optimal habitats. Such a threshold reduces the possibility of false-positives (Buhl-Mortensen et al., 2019). For potentially suitable habitats, we used a fixed threshold of 0.5 (Elith et al., 2010; Kramer-Schadt et al., 2013). The complementary log-log (cloglog) transform was used to build the models as the best fit for estimating the occurrence probability (Phillips et al., 2017). Distribution maps were generated with a scale of species occurrence probability from 0 to 1 in the Maxent palette colour gradations.

The climatogenic distribution dynamics of *Fritillaria latifolia* was considered in four time periods, namely 2021–2040, 2041–2060, 2061–2080, 2081–2100. We used the UKESM1-0-LL (UK Earth System Model) developed in the United Kingdom at the CMIP6 project (Sellar et al., 2019). This is the second highest priority model in the ISIMIP3b modelling protocol (Lange & Büchner, 2020). For this model, we considered two general socio-economic pathways (SSP), in particular the optimistic scenario SSP1-2.6 and the worst-case scenario SSP5-8.5. The calculation of ENVIREM layers for these scenarios were shown in Data/Predictor variables/Data processing of the ODMAP protocol (Electronic Supplement 4). In total, we built eight climatic BA-models of *Fritillaria latifolia* future distribution under two scenarios in four time periods. The anthropogenic and orographic predictors were assumed constant.

The localisation of *Fritillaria latifolia* refugia with a consistently high probability of the species occurrence despite climatic changes was determined in several steps. First, we converted into points the optimal sites of the species occurrence at present. Second, at these points we extracted values of the species occurrence probability in future time periods. Third, on the raster layers of the climatic BA-models, we cut off points with the occurrence probability below 0.8. Finally, we mapped areas where the probability of *Fritillaria latifolia* occurrence exceeded 0.8 throughout the prediction period.

Results

Selection of the most suitable set of environmental variables. A-models

The performance statistics of the resulting WorldClim2+GMTED2010 and ENVIREM A-models indicated their high predictive accuracy (Electronic Supplement 2: Table S4). According to the first A-model, the current *Fritillaria latifolia* distribution was influenced by climatic factors such as maximum mean temperature in February, precipitation in November, and by altitude (Table 1). Predicted altitude values (0.8 threshold) corresponded to the altitude values in *Fritillaria latifolia* habitats, reported previously, namely 1600–2300 m a.s.l. in Abkhazia (Tania & Abramova, 2013), 1700–2500 m a.s.l. in Armenia (Batsatsashvili et al., 2017), 2100–2500 m a.s.l. in the Central Caucasus (Pshegusov et al., 2019).

As reported in the Red Data Book of the Chechen Republic (2020), *Fritillaria latifolia* occurs at altitudes up to 3000 m a.s.l. in the Eastern Caucasus. The main processes of underground morphogenesis and growth of the species occur in late winter, while the main processes of aboveground vegetation (sprouting, shoot growth, flowering) take place in spring (Thazaplizheva & Chadaeva, 2012). This probably explains the importance of maximum mean temperature in February in the *F. latifolia* distribution. A suitable temperature range during this critical vegetation period is typical for the mountainous regions of the Western Caucasus and Western Transcaucasia. Accordingly, the model predicted the *F. latifolia* core range in these areas (Fig. 2a), which is consistent with field observations (Pshegusov et al., 2019). At the same time, an interpretation of the November precipitation influence, i.e. precipitation during the species dormancy period, was difficult.

According to the ENVIREM A-model, the most important variable in the species distribution was Emberger's pluviothermic quotient, with optimal values corresponding to humid and perhumid climates (Daget et al., 1988) (Table 1). The model predicted the core ranges of this hydrophilic species in the Western Caucasus, Western and Central Transcaucasia, and the western ridges of the Lesser Caucasus (Fig. 2b), i.e. in areas with humid subtropical and oceanic climate (Fig. 1b).

Table 1. Contribution of the main abiotic variables (percentage contribution of more than 10%) to the WorldClim2+GMTED2010 and ENVIREM A-models of *Fritillaria latifolia* ecological niche

WorldClim2+GMTED2010			ENVIREM		
Variable	PC, %	Optimal values	Variable	PC, %	Optimal values
tmax2, °C	31.6	from -4 to +0	embergerQ	54.7	150–190
prec11, mm	29.5	135–155	TRI	20.8	75–250
Alt, m a.s.l.	11.4	1800–2100	PETColdestQuarter, mm/month	14	7–14

Note: Predictor abbreviations: tmax2 – maximum mean temperature in February, prec11 – precipitation in November, Alt – altitude, embergerQ – Emberger's pluviothermic quotient, TRI – terrain roughness index, PETColdestQuarter – mean monthly potential evapotranspiration of the coldest quarter. Variable importance is represented as a percentage contribution (PC, %) in the Maxent models. Optimal values of variables were sourced from the response curves by cutting off at the threshold of 0.8.

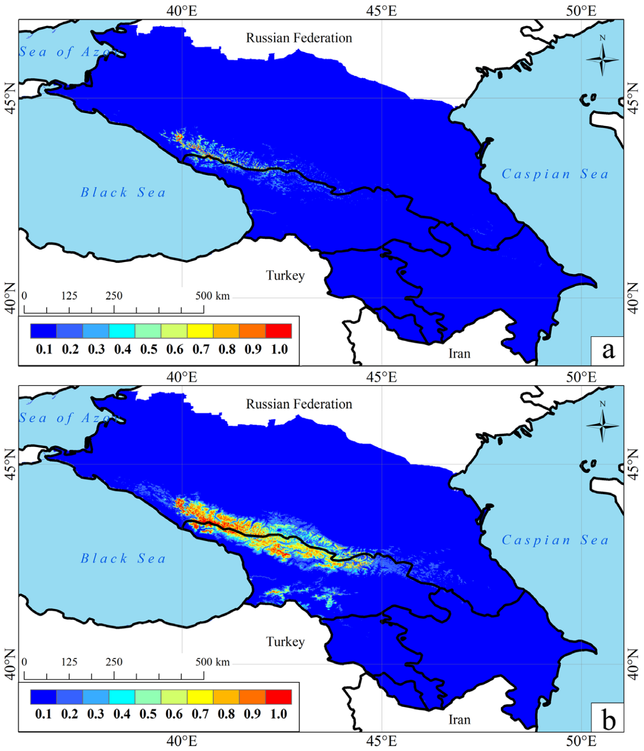

Fig. 2. Predictive maps of the *Fritillaria latifolia* distribution in the Caucasus by A-models based on WorldClim2+GMTED2010 (a) and ENVIREM (b) sets of environmental variables. Designations: 0–1 scale indicates the probability of species occurrence.

Less suitable habitat conditions were predicted in the humid Central Caucasus, while unsuitable habitats were expected in the arid areas of the Ciscaucasia, the eastern part of the Greater and Lesser Caucasus, the Transcaucasian Highland and the Kura-Araks Lowland. The second most important predictor of *Fritillaria latifolia* distribution was the terrain roughness index, with optimal values ranging from nearly level (81–116) to intermediately rugged (162–239) slopes (Riley et al., 1999). This is in line with field studies showing that the species is mainly distributed in relatively gentle terrain (Tania & Abramova, 2013; Pshegusov et al., 2019).

As a result, in both A-models (WorldClim2+GMTED2010 and ENVIREM) the contribution and optimal values of environmental predictors were largely consistent with the ecological features of *Fritillaria latifolia*, and the predictive distribution maps were in line with the actual localisation of species populations. In both A-models, the three most important predictors were temperature, humidity and orographic parameters. Despite similar results, we concluded that the ENVIREM cartographic model was more consistent with the actual distribution of *Fritillaria latifolia* in the Caucasus. Compared to the more «strict» WorldClim2+GMTED2010 A-model, it predicted large suitable areas in Transcaucasia, which is in agreement with literature data on *Fritillaria latifolia* occurrence in northern parts of Abkhazia and Georgia and in northwestern part of Armenia (Tania & Abramova, 2013; Batsatsashvili et al., 2017). Furthermore, ENVIREM predictors are not difficult to interpret from available scales, and they have a direct link to physiological and ecological processes in vegetation cover (Title & Bemmels, 2018). Emberger's pluviothermic quotient and terrain roughness index combine highly correlated variables in mountainous areas (altitude and slope steepness, temperature and evapotranspiration). In our view, their use contributes to addressing the high collinearity of environmental variables that have coherent variability on the altitude gradient in mountains. In addition, as shown above, no sampling bias problems have been identified for ENVIREM A-model only. Accordingly, we used the set of ENVIREM variables to build the models of *Fritillaria latifolia* distribution (Electronic Supplement 1).

BA- and BAM-models of Fritillaria latifolia distribution

High values of AUCtest, CBItest and TSStest were obtained for the models (Table 2). These values indicated high predictive accuracy of the resulting models (good balance between model accuracy and complexity, and model sensitivity and specificity in discriminating occurrence data from random data).

As shown in Table 1, the main abiotic predictors in the A-model of *Fritillaria latifolia* distribution were embergerQ and TRI, which determine the location of optimal habitats on near-level and intermediately rugged slopes in humid and perhumid climate. These climatic and orographic parameters also contributed most to the BA-model (Table 2). Accordingly, the differences in areas of suitable and optimum habitats predicted by the A-model and BA-model were only 0.44% and 0.02% of the study area (1700 km^2 and 80 km^2), respectively (Table 3).

In terms of the percentage contribution to the BA-model, the distance to Protected Areas was the third important factor with optimal values of 0–1 km. This probably explains the increase in the species optimal habitats according to the BA-model (Table 3, Fig. 3a). The grazing factor, formalised through the distance to grasslands, contributed less to the model. *Fritillaria latifolia* populations could be found both within grasslands and 40 km away from grasslands (Table 2).

Table 2. Model performance and contribution of the main variables to the Maxent models of *Fritillaria latifolia* distribution in the Caucasus

Environmental variables	A-model		BA-model		BAM-model	
	PC, %	Optimal values	PC, %	Optimal values	PC, %	Optimal values
embergerQ	54.7	150–190	48.7	160–180	28.1	160–180
TRI	20.8	75–250	19.8	80–250	15.9	80–250
PETColdestQuarter, mm/month	14.0	7–14	8.7	5–14	2.6	5–14
path_PAs, km	–	–	14.7	0–1	5.3	0–1
path_landuse, km	–	–	1.5	0–40	0.3	0–20
Movement factor, km	–	–	–	–	44.5	0–15
AUCtest ± SD	0.95 ± 0.02		0.97 ± 0.01		0.97 ± 0.01	
CBItest	0.93		0.96		0.93	
TSStest	0.82		0.85		0.86	

Note: Predictor abbreviations: embergerQ – Emberger's pluviothermic quotient, TRI – terrain roughness index, PETColdestQuarter – mean monthly potential evapotranspiration of the coldest quarter, path_Pas – distance to Protected Areas, path_landuse – distance to grasslands. Model performance was assessed by AUCtest (area under the curve from validation datasets) values averaged over five replications, CBItest (continuous Boyce index from validation datasets), and TSStest (true skill statistics from validation datasets).

Table 3. Areas of suitable and optimal habitats of *Fritillaria latifolia* based on the Maxent models

Suitable areas, percentage of the study area			Optimal areas, percentage of the study area		
A-model	BA-model	BAM-model	A-model	BA-model	BAM-model
2.04	1.60	1.85	0.71	0.73	0.94

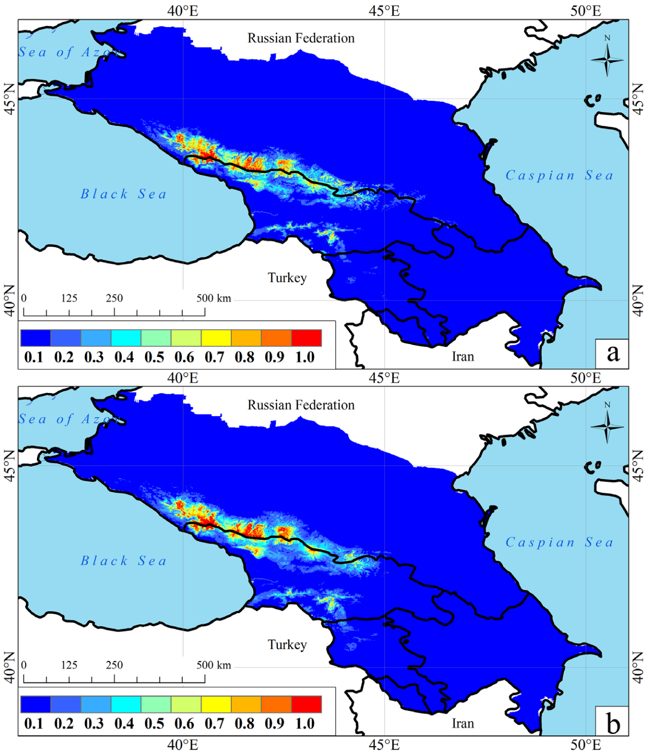

Fig. 3. Predictive maps of *Fritillaria latifolia* distribution in the Caucasus based on BA-model (a) and BAM-model (b).

According to the BAM-model, an important predictor of *Fritillaria latifolia* distribution was the movement factor (area accessibility) with a percentage contribution equal to the combined contribution of abiotic variables (Table 2). The distance of suitable areas to optimal habitats was 15 km, and the area of suitable and optimal areas increased by 0.25% and 0.21% of the study area (980 km^2 and 830 km^2), respectively, compared to the BA-model (Table 3, Fig. 3b).

Climatogenic dynamics of the Fritillaria latifolia range

Optimistic SSP1-2.6 models predicted a 1.6-fold decrease in the area of suitable and optimal habitats of *Fritillaria latifolia* from 2021 to 2100. The pessimistic (worst-case) SSP5-8.5 models predicted a 103-fold reduction in suitable habitat areas and a 122-fold reduction in optimal habitat areas (Table 4).

According to both scenarios, the reduction in habitat area was particularly pronounced in the western part of the current species range with the most humid (subtropical and oceanic) climate (Electronic Supplement 2: Fig. S2). The climatic models predicted less habitat reduction in the Central Caucasus with a humid continental climate. In the pessimistic scenario, only a small core range of *Fritillaria latifolia* would remain here by 2080 and 2100. The optimistic models predicted that the species core ranges would remain in the highlands of the Western and Central Caucasus (Electronic Supplement 2: Fig. S2).

Given the species dependence on the climatic parameters (Table 2), the predicted reduction in its range is explained by a decrease in embergerQ and annual precipitation with a simultaneous increase in mean annual temperature (Fig. 4). By 2060 and 2100, the worst-case SSP5-8.5 scenario predicted an increase in average annual temperature of 6°C and 9°C and a decrease in annual precipitation of 30 mm and 40 mm, respectively. The SSP5-8.5 scenario predicted only 7 km^2 (0.002% of the study area) of *Fritillaria latifolia* refugia by 2060 and no consistently optimal areas by 2080 (Electronic Supplement 2: Table S5).

Table 4. Habitat areas of *Fritillaria latifolia* according to the climatic models based on the optimistic (SSP1-2.6) and the worst-case (SSP5-8.5) socio-economic pathways during 2021–2100

Climatic models	SSP1-2.6				SSP5-8.5			
	2021–2040	2041–2060	2061–2080	2081–2100	2021–2040	2041–2060	2061–2080	2081–2100
Suitable areas, percentage of the study area	1.20	0.84	0.85	0.76	1.06	0.26	0.06	0.01
Optimal areas, percentage of the study area	0.37	0.22	0.27	0.23	0.31	0.05	0.01	0.002

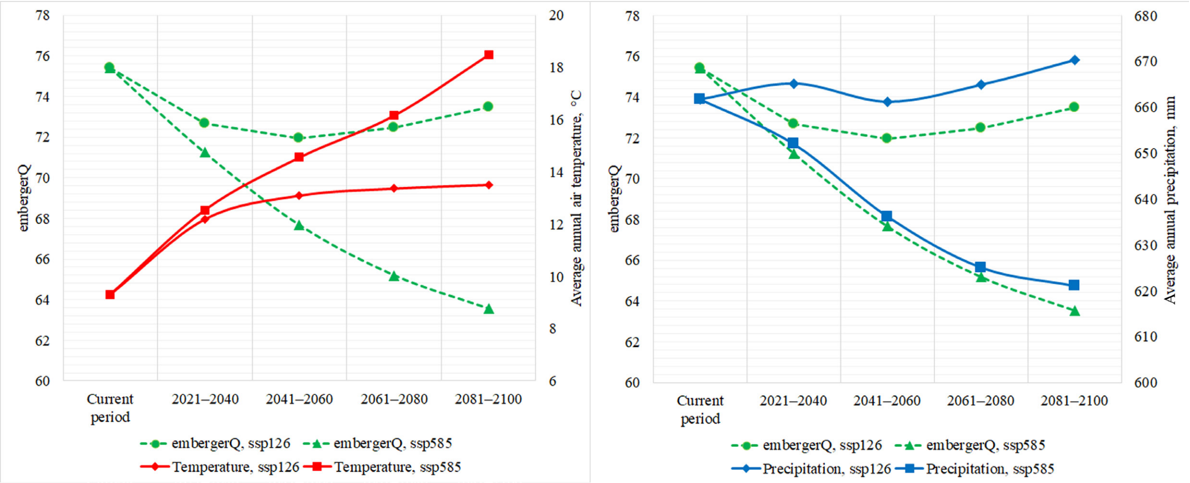

Fig. 4. Dynamics of embergerQ, average annual temperature and average annual precipitation in the Caucasus according to the climate change scenarios (socio-economic pathways) SSP1-2.6 and SSP5-8.5.

According to the optimistic SSP1-2.6 model, by 2100 the refugia area would be 172.4 km^2 (0.05% of the study area) (Electronic Supplement 2: Table S5), and three main refugia of *Fritillaria latifolia* will remain in the highlands of the Western and Central Caucasus (Fig. 5). The refugia will be partly located within Protected Areas.

Discussion

Previous studies covered various aspects of *Fritillaria latifolia* ecology, such as orographic and climatic requirements for habitats (Tania & Abramova, 2013; Yamalov et al., 2014; Batsatsashvili et al., 2017; Pshegusov et al., 2019), seasonal vegetation (Thazaplizheva & Chadaeva, 2012), the actual localisation of the species in the Caucasus (Zernov, 2006; Zernov & Onipchenko, 2011; Tania & Abramova, 2013; Pshegusov et al., 2019), its population biology (Thazaplizheva & Chadaeva, 2012; Tania & Abramova, 2013; Pshegusov et al., 2019). Although most of these surveys were carried out using field observations, our study can be seen in the context of previous investigations. We assessed the potential distribution of *Fritillaria latifolia* in relation to abiotic and anthropogenic factors, area accessibility and climate changes. This provided new insights into the importance of Protected Areas as the species refugia in the Caucasus.

Current distribution of Fritillaria latifolia

According to the A-, BA- and BAM-models, the optimal habitats of *Fritillaria latifolia* in the Caucasus were located on relatively gentle, wet slopes (Table 2), which is consistent with field observations (Tania & Abramova, 2013; Yamalov et al., 2014; Batsatsashvili et al., 2017; Pshegusov et al., 2019). The occurrence of this hydrophilic species was predicted mainly in areas with humid subtropical and oceanic climate, such as the Western Caucasus, Western and Central Transcaucasia, and the western ridges of the Lesser Caucasus (Fig. 2, Fig. 3). The lack of suitable sites in the Colchis Lowland with a humid climate was probably due to the species preference for highlands (Tania & Abramova, 2013; Yamalov et al., 2014; Pshegusov et al., 2019; Batsatsashvili et al., 2017).

The optimal habitats of *Fritillaria latifolia* predicted within 0–1 km of the Protected Areas (Table 2). Actually, the main reported habitats of this species in Abkhazia were concentrated within the Ritsa Relict National Park (Tania & Abramova, 2013), while species populations in northwestern Armenia were localised in the Lake Arpi National Park (Batsatsashvili et al., 2017). In the North Caucasus, *Fritillaria latifolia* was also mainly found within a network of Protected Areas covering most of the highlands. There are the Sochi National Park and Teberda National Park (Zernov, 2006; Zernov & Onipchenko, 2011), Prielbrusye National Park

(Pshegusov et al., 2019), Erzi State Nature Reserve, and Argun State Museum-Reserve (Red Data Book of the Chechen Republic, 2020). Suitable species habitats in northern Georgia, particularly in Racha-Lechkhumi Region, Svaneti Region and Mtiuleti Region (Batsatsashvili et al., 2017), were mostly located outside Protected Areas. This probably explains the considerable reduction in the species optimal habitats in this area according to the BA-model (Fig. 3a), although in the total area of optimal habitats it is increased based on the A-model (Table 3).

The low contribution of the grazing factor in the tested models (Table 2) may be associated with the resistance of *Fritillaria latifolia* to trampling by animals. This resistance is probably related to the protected underground bulbs (Yamalov et al., 2014) and the early vegetation season before cattle moving to summer pastures (Taniya & Abramova, 2013). Moderate grazing may also positively affect the species population parameters (bulb and seed reproduction, population density) by reducing vegetation coverage and the level of interspecific competition in the plant community (Thazaplizheva & Chadaeva, 2012; Pshegusov et al., 2019).

The species mobility (area accessibility) was 15 km to optimal habitats (Table 2). Ecologically, the area accessibility (the vastness of suitable subalpine grasslands) explains the species dispersal capacity on a 15-km scale. Biologically, the species distribution ability is related to seed spreading by wind and water. Despite the abundance of geographical barriers in the mountains, this species mobility resulted in an increase in the area of suitable and optimal habitats of *Fritillaria latifolia* in the BAM-model.

Future species distribution against the background of climate changes. Climatic refugia

Fritillaria latifolia belongs to the psychrophytes, which prefer cold and wet habitats (Red Data Book of the Chechen Republic, 2020). Therefore, an increase in climate aridity (Fig. 4) is considered a major limiting factor for the species, which is consistent with our results. The Central Caucasus, with its humid continental climate, is probably more resistant to climate changes than the Western Caucasus, Western and Central Transcaucasia, and the western ridges of the Lesser Caucasus with the most humid climate. The main future core ranges of the species were predicted in the Central Caucasus under both worst-case and optimistic socio-economic pathways (Electronic Supplement 2: Fig. S2).

Species refugia (areas with a consistently high probability of *Fritillaria latifolia* occurrence despite climate change) by 2100 under the SSP1-2.6 scenario were projected in the highlands of the Western and Central Caucasus (Fig. 5). The Western Caucasus refugia are partly located within the Caucasus State Nature Reserve and Teberda National Park. The Central Caucasus refugia are located within the Prielbrusye National Park. These areas should be prioritised for the conservation of *Fritillaria latifolia* populations in the Caucasus.

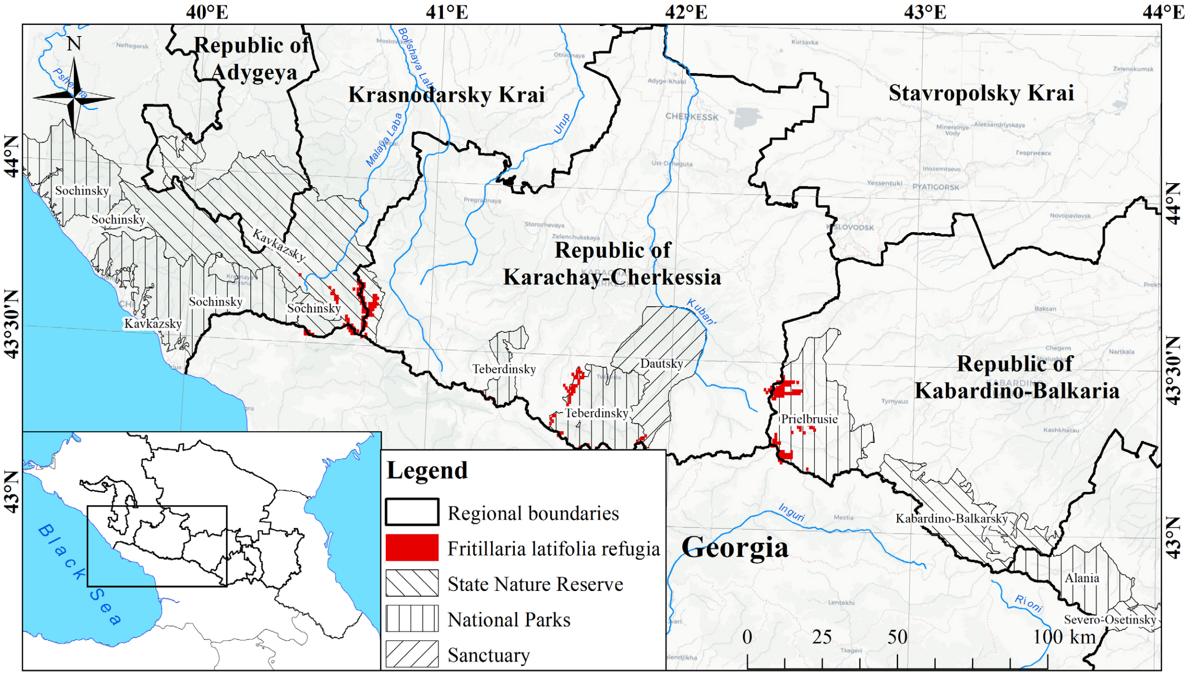

Fig. 5. The predicted location of *Fritillaria latifolia* refugia in the Caucasus by 2100 according to the optimistic SSP1-2.6 scenario.

Conclusions

For the first time using SDM, the influence of abiotic, anthropogenic factors and area accessibility on the current and future distribution of *Fritillaria latifolia* in the Caucasus was studied, and the territories prioritised for the species conservation were identified. ENVIREM and WorldClim2+GMTED2010 models of the *Fritillaria latifolia* ecological niche had good performance indicators and were largely consistent with the ecological and biological characteristics of the species. However, the ENVIREM model was more in line with the actual localisation of the species and had no sampling bias problem. Accordingly, we used the ENVIREM set of variables to construct BAM-models.

The main abiotic predictors of *Fritillaria latifolia* distribution in the Caucasus were Emberger's pluviothermic quotient and terrain roughness index. The importance (percentage contribution) of these predictors was also high in the BA-model, which considered distances to Protected Areas and grasslands, and in the BAM-model, which included an area accessibility factor. Optimal *Fritillaria latifolia* habitats occurred on nearly level to intermediately rugged mountain slopes in humid and perhumid climates no more than 0–1 km to the Protected Areas, and the area accessibility of the species was about 15 km. At present the potential area of optimal habitats for the species is 3680 km^2 or 0.94% of the study area. Optimistic models predicted a 1.6-fold decrease in the area of optimal *Fritillaria latifolia* habitats by 2100, while pessimistic models predicted a 122-fold decrease, respectively.

The results also confirmed our hypothesis that distance to Protected Areas is one of the key factors in the current and future distribution of *Fritillaria latifolia*. Species core ranges are localised in the Western and Central Caucasus, Western and Central Transcaucasia, and the northwestern ridges of the Lesser Caucasus within a network of Protected Areas covering most of the highlands. Given the extensive tourism development in the Caucasus, strict monitoring of the environmental regime in these territories is required. According to the optimistic models, refugia with a consistently high probability of *Fritillaria latifolia* occurrence by 2080–2100 would remain in the highlands of the Western and Central Caucasus, including the Caucasus State Nature Reserve and Teberda National Park. These Protected Areas are a priority for the species conservation in the Caucasus, and their identification constitutes the practical importance of the study. Future studies should be aimed at monitoring of the condition of *Fritillaria latifolia* populations, searching for new species localities in the predicted areas, as well as adjusting forecasts to new climate change scenarios.

Acknowledgements

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Supporting Information

Additional data for the paper by Phegusov & Chadaeva (2024), with four Electronic Supplements, may be found in the **Supporting Information**.

References

Aiello-Lammens M.E., Boria R.A., Radosavljevic A., Vilela B., Anderson R.P. 2015. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography* 38(5): 541–545. DOI: 10.1111/ecog.01132

Amatulli G., Domisch S., Tuanmu M.N., Parmentier B., Ranipeta A., Malczyk J., Jetz W. 2018. A suite of global, cross-scale topographic variables for environmental and biodiversity modeling. *Scientific Data* 5: 180040. DOI: 10.1038/sdata.2018.40

Atayev Z.V., Bratkov V.V. 2014. Reaction of landscapes of the North Caucasus on the current climatic changes. *South of Russia: Ecology, Development* 9(1): 141–157. DOI: 10.18470/1992-1098-2014-1-141-157 [In Russian]

Banag C., Thrippleton T., Alejandro G.J., Reineking B., Liede-Schumann S. 2015. Bioclimatic niches of selected endemic Ixora species on the Philippines: predicting habitat suitability due to climate change. *Plant Ecology* 216(9): 1325–1340. DOI: 10.1007/s11258-015-0512-6

Batsatsashvili K., Kikvidze Z., Khutsishvili M., Maisaia I., Sikharulidze Sh., Tchelidze D., Zambrana N.Y.P., Bussmann R.W. 2017. *Fritillaria collina* Adams, Liliaceae. In: R.W. Bussmann (Ed.): *Ethnobotany of the Caucasus. European Ethnobotany*. Cham: Springer. P. 209–311.

Bowen A.K.M., Stevens M.H.H. 2020. Temperature, topography, soil characteristics, and NDVI drive habitat preferences of a shade-tolerant invasive grass. *Ecology and Evolution* 10(19): 10785–10797. DOI: 10.1002/ece3.6735

Buhl-Mortensen L., Burgos J.M., Steingrund P., Buhl-Mortensen P., Ólafsdóttir S.H., Ragnarsson S.Á. 2019.

Vulnerable marine ecosystems (VMEs): Coral and sponge VMEs in Arctic and sub-Arctic waters – Distribution and threats. Copenhagen: Nordisk Ministerråd. 144 p. DOI: 10.6027/TN2019-519

Christmas M.J., Breed M.F., Lowe A.J. 2016. Constraints to and conservation implications for climate change adaptation in plants. *Conservation Genetics* 17(2): 305–320. DOI: 10.1007/s10592-015-0782-5

Clark P.J., Evans F.C. 1954. Distance to Nearest Neighbor as a Measure of Spatial Relationships in Populations. *Ecology* 35(4): 445–453. DOI: 10.2307/1931034

Conrad O., Bechtel B., Bock M., Dietrich H., Fischer E., Gerlitz L., Wehberg J., Wichmann V., Böhner J. 2015. System for Automated Geoscientific Analyses (SAGA) v. 2.1.4. *Geoscientific Model Development* 8(7): 1991–2007. DOI: 10.5194/gmd-8-1991-2015

Daget P., Ahdali L., David P. 1988. Mediterranean bioclimate and its variation in the Palaearctic region. In: Specht R.L. (Ed.): *Mediterranean-type Ecosystems. Tasks for vegetation science*. Vol. 19. Dordrecht: Springer. P. 139–148. DOI: 10.1007/978-94-009-3099-5_6

Danielson J.J., Gesch D.B. 2011. *Global multi-resolution terrain elevation data 2010 (GMTED2010)*. U.S. Geological Survey Open-File Report 2011–1073. Reston, Virginia, USA: U.S. Geological Survey. 26 p.

Duarte A., Whitlock S.L., Peterson J.T. 2019. Species Distribution Modeling. In: Fath B. (Ed.): *Encyclopedia of Ecology (Second Edition)*. Vol. 2. Amsterdam: Elsevier. P. 189–198. DOI: 10.1016/B978-0-12-409548-9.10572-X

Elith J., Graham C.H., Anderson R.P., Dudik M., Ferrier S., Guisan A., Hijmans R.J., Huettmann F., Leathwick J.R., Lehmann A., Li J., Lohmann L.G., Loiselle B.A., Manion G., Moritz C., Nakamura M., Nakazawa Y., Overton J.McC.M., Peterson A.T., Phillips S.J., Richardson K., Scachetti-Pereira R., Schapire R.E., Soberón J., Williams S., Wisz M.S., Zimmermann N.E. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29(2): 129–151. DOI: 10.1111/j.2006.0906-7590.04596.x

Elith J., Kearney M., Phillips S. 2010. The art of modelling range-shifting species. *Methods in Ecology and Evolution* 1(4): 330–342. DOI: 10.1111/j.2041-210X.2010.00036.x

Elith J., Phillips S.J., Hastie T., Dudík M., Chee Y.E., Yates C.J. 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* 17(1): 43–57. DOI: 10.1111/j.1472-4642.2010.00725.x

ENVIREM. 2023. *ENVIronmental Rasters for Ecological Modeling*. Available from https://envirem.github.io/

Fick S.E., Hijmans R.J. 2017. WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37(12): 4302–4315. DOI: 10.1002/joc.5086

GBIF.org. 2023. *GBIF Occurrence Download*. Available from https://doi.org/10.15468/dl.fmvp6e

Glover-Kapfer P.A. 2015. *A training manual for habitat suitability and connectivity modeling using tigers (Panthera tigris) in Bhutan as example. Technical Report*. Bhutan: WWF. 46 p. DOI: 10.13140/RG.2.2.34804.86409

GMTED2010. 2023. *GMTED2010 U.S. Geological Survey (usgs.gov)*. Available from https://www.usgs.gov/coastal-changes-and-impacts/gmted2010

Guerrina M., Conti E., Minuto L., Casazza G. 2016. Knowing the past to forecast the future: a case study on a relictual, endemic species of the SW Alps, Berardia subacaulis. *Regional Environmental Change* 16(4): 1035–1045. DOI: 10.1007/s10113-015-0816-z

Ji L., Gallo K. 2006. An agreement coefficient for image comparison. *Photogrammetric Engineering and Remote Sensing* 72(7): 823–833. DOI: 10.14358/PERS.72.7.823

Kramer-Schadt S., Niedballa J., Pilgrim J.D., Schröder B., Lindenborn J., Reinfelder V., Stillfried M., Heckmann I., Scharf A.K., Augeri D.M., Cheyne S.M., Hearn A.J., Ross J., Macdonald D.W., Mathai J., Eaton J., Marshall A.J., Semiadi G., Rustam R., Bernard H., Alfred R., Samejima H., Duckworth J.W., Breitenmoser-Wuersten C., Belant J.L., Hofer H., Wilting A. 2013. The importance of correcting for sampling bias in MaxEnt species distribution models. *Diversity and Distributions* 19(11): 1366–1379. DOI: 10.1111/ddi.12096

Lange S., Büchner M. 2020. *ISIMIP3b bias-adjusted atmospheric climate input data (1.1)*. ISIMIP Repository. DOI: 10.48364/ISIMIP.842396.1

Liu C., White M., Newell G. 2013. Selecting thresholds for the prediction of species occurrence with presence-only data. *Journal of Biogeography* 40(4): 778–789. DOI: 10.1111/jbi.12058

Mazangi A., Ejtehadi H., Mirshamsi O., Ghassemzadeh F., Hosseinianyousefkhani S.S. 2016. Effects of climate change on the distribution of endemic *Ferula xylorhachis* Rech.f. (Apiaceae: Scandiceae) in Iran: Predictions from ecological niche models. *Russian Journal of Ecology* 47(4): 349–354. DOI: 10.1134/S1067413616040123

McCoy J., Johnston K., Kopp S., Borup B., Willison J., Payne B. 2001. *Using ArcGIS spatial analyst*. Redlands: ESRI Press. 232 p.

Merow C., Smith M.J., Silander J.A. 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* 36(10): 1058–1069. DOI: 10.1111/j.1600-0587.2013.07872.x

NextGIS. 2023. *Vector layers and ready-to-go GIS projects based on OSM in ESRI Shape, Geodatabase*. Available from https://data.nextgis.com

Ortiz-Urbina E., Diaz-Balteiro L., Iglesias-Merchan C. 2020. Influence of Anthropogenic Noise for Predicting Cinereous Vulture Nest Distribution. *Sustainability* 12(2): 503. DOI: 10.3390/su12020503

Pearson R.G., Dawson T.P., Lin C. 2004. Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. *Ecography* 27(3): 285–298. DOI: 10.1111/j.0906-7590.2004.03740.x

Peel M.C., Finlayson B.L., Mcmahon T.A. 2007. Updated world map of the Köppen-Geiger climate classification.

Hydrology and Earth System Sciences 11(5): 1633–1644. DOI: 10.5194/hess-11-1633-2007

Peterson A.T. 2006. Uses and requirements of ecological niche models and related distributional models. *Biodiversity Informatics* 3: 59–72. DOI: 10.17161/bi.v3i0.29

Peterson A.T., Soberón J. 2012. Species Distribution Modeling and Ecological Niche Modeling: Getting the Concepts Right. *Natureza e Conservação* 10(2): 102–107. DOI: 10.4322/natcon.2012.019

Peterson A.T., Soberón J., Pearson R.G., Anderson R.P., Martínez-Meyer E., Nakamura M., Araújo M.B. 2011. *Ecological Niches and Geographic Distributions (MPB-49)*. Princeton: Princeton University Press. 329 p. DOI: 10.1515/9781400840670

Petrosyan V., Osipov F., Bobrov V., Dergunova N., Omelchenko A., Varshavskiy A., Danielyan F., Arakelyan M. 2020. Species Distribution models and niche partitioning among unisexual *Darevskia dahli* and its parental bisexual (*D. portschinskii*, *D. mixta*) rock lizards in the Caucasus. *Mathematics* 8(8): 1329. DOI: 10.3390/math8081329

Phillips S.J., Dudík M. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31(2): 161–175. DOI: 10.1111/j.0906-7590.2008.5203.x

Phillips S.J., Anderson R.P., Dudík M., Schapire R.E., Blair M.E. 2017. Opening the black box: An open-source release of Maxent. *Ecography* 40(7): 887–893. DOI: 10.1111/ecog.03049

Pshegusov R.H., Chadaeva V.A., Taniya I.V., Abramova L.M., Mustafina A.N. 2019. Life strategies and the long-term climate-driven dynamics of the endemic Caucasian plant *Fritillaria latifolia* Willd. *Uchenye Zapiski Kazanskogo Universiteta. Seriya Estestvennye Nauki* 161(4): 571–589. DOI: 10.26907/2542-064X.2019.4.571-589 [In Russian]

Pshegusov R., Tembotova F., Chadaeva V., Sablirova Y., Mollaeva M. Akhomgotov A. 2022. Ecological niche modeling of the main forest-forming species in the Caucasus. *Forest Ecosystems* 9: 100019. DOI: 10.1016/j.fecs.2022.100019

Qin A., Liu B., Guo Q., Bussmann R.W., Ma F., Jian Z., Xu G., Pei S. 2017. Maxent modeling for predicting impacts of climate change on the potential distribution of *Thuja sutchuenensis* Franch., an extremely endangered conifer from southwestern China. *Global Ecology and Conservation* 10: 139–146. DOI: 10.1016/j.gecco.2017.02.004

R Core Team. 2023. *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available from https://www.R-project.org

Red Data Book of the Republic of Kabardino-Balkaria. Nalchik: Pechatnyy dvor, 2018. 496 p. [In Russian]

Red Data Book of the Chechen Republic (second edition). Rostov-on-Don: Yuzhnyy Publisher House, 2020. 480 p. [In Russian]

Riemann R., Wilson B.T., Lister A., Parks S. 2010. An effective assessment protocol for continuous geospatial datasets of forest characteristics using USFS Forest Inventory and Analysis (FIA) data. *Remote Sensing of Environment* 114(10): 2337–2352. DOI: 10.1016/j.rse.2010.05.010

Riley S.J., DeGloria S.D., Elliot R. 1999. A Terrain Ruggedness Index that quantifies topographic heterogeneity. *Intermountain Journal of Sciences* 5(1–4): 23–27.

Sellar A.A., Jones C.G., Mulcahy J.P., Tang Y., Yool A., Wiltshire A., O’Connor F.M., Stringer M., Hill R., Palmieri J., Woodward S., de Mora L., Kuhlbrodt T., Rumbold S.T., Kelley D.I., Ellis R., Johnson C.E., Walton J., Abraham N.L., Andrews M.B., Andrews T., Archibald A.T., Berthou S., Burke E., Blockley E., Carslaw K., Dalvi M., Edwards J., Folberth G.A., Gedney N. et al. 2019. UKESM1: Description and evaluation of the U.K. Earth System Model. *Journal of Advances in Modeling Earth Systems* 11(12): 4513–4558. DOI: 10.1029/2019MS001739

Sharma H.P., Dhakal S., Bhusal K.P., Dhakal H., Gautam R., Joshi A.B., Rana D.B., Ghimire M., Ghimire S., Belant J.L. 2023. Factors influencing the potential distribution of globally endangered Egyptian Vulture nesting habitat in Nepal. *Animals* 13(4): 633. DOI: 10.3390/ani13040633

Sillero N., Arenas-Castro S., Enriquez-Urzelai U., Vale C.G., Sousa-Guedes D., Martínez-Freiría F., Real R., Barbosa A.M. 2021. Want to model a species niche? A step-by-step guideline on correlative ecological niche modelling. *Ecological Modelling* 456: 109671. DOI: 10.1016/j.ecolmodel.2021.109671

Soberón J., Peterson A. 2005. Interpretation of models of fundamental ecological niches and species’ distributional areas. *Biodiversity Informatics* 2: 1–10. DOI: 10.17161/bi.v2i0.4

Soberón J., Osorio-Olvera L. 2023. A dynamic theory of the area of distribution. *Journal of Biogeography* 50(6): 1037–1048. DOI: 10.1111/jbi.14587

Syfert M.M., Smith M.J., Coomes D.A. 2013. The effects of sampling bias and model complexity on the predictive performance of maxent species distribution models. *PLoS ONE* 8(2): e55158. DOI: 10.1371/journal.pone.0055158

Tania I.V., Abramova L.M. 2013. Rare species of the highest plants of Ritsinsky Relic National Park (Abkhazia Republic). *Proceedings of Samara Scientific Center of RAS* 15(3): 1457–1461. [In Russian]

Thazaplizheva L.Kh., Chadaeva V.A. 2012. Survival strategies of some species of geophytes in the Area of the Kabardino-Balkar Republic. *Uchenye Zapiski Kazanskogo Universiteta. Seriya Estestvennye Nauki* 154(4): 199–205. [In Russian]

Title P.O., Bemmels J.B. 2018. ENVIREM: an expanded set of bioclimatic and topographic variables increases flexibility and improves performance of ecological niche modeling. *Ecography* 41(2): 291–307. DOI: 10.1111/ecog.02880

Van Dyke F. 2008. *Conservation Biology. Foundations, Concepts, Applications*. Dordrecht: Springer. 478 p. DOI: 10.1007/978-1-4020-6891-1

Vignali S., Lörcher F., Hegglin D., Arlettaz R., Braunisch V. 2021. Modelling the habitat selection of the bearded vulture to predict areas of potential conflict with wind energy development in the Swiss Alps. *Global Ecology and Conservation* 25: e01405. DOI: 10.1016/j.gecco.2020.e01405

WorldClim2. 2023. *WorldClim climate data base*. Available from https://worldclim.com/version2

Yamalov S.M., Tania I.V., Khasanova G.R., Kuropatkin V.V. 2014. Ordination of grass communities with *Fritillaria latifolia* in the Ritsinsky Relic National Park (Abkhazia). *Proceedings of the RAS Ufa Scientific Centre* 3: 108–112. [In Russian]

Zernov A.S. 2006. *Flora of the North-West Caucasus*. Moscow: KMK Scientific Press Ltd. 664 p. [In Russian]

Zernov A.S., Onipchenko V.G. 2011. *Vascular plants of the Republic of Karachay-Cherkessia (flora synopsis)*. Moscow: MAKS Press. 240 p. [In Russian]

МОДЕЛИРОВАНИЕ ПРОСТРАНСТВЕННОГО РАСПРОСТРАНЕНИЯ КАВКАЗСКОГО ЭНДЕМИКА *FRITILLARIA LATIFOLIA* НА ФОНЕ КЛИМАТИЧЕСКИХ ИЗМЕНЕНИЙ

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Современные изменения климата, деградация местообитаний, перевыпас скота, сбор побегов и луковиц представляют серьезную угрозу для редкого кавказского эндемика *Fritillaria latifolia*. Изучение лимитирующих факторов и динамики ареала вида в связи с изменением климата и роли особо охраняемых природных территорий в распространении необходимо для разработки эффективной системы сохранения вида в настоящее время и в будущем. Целями данного исследования были: (1) определить наиболее подходящий набор абиотических предикторов для моделирования локализации *Fritillaria latifolia*, (2) формализовать абиотические и антропогенные факторы в моделях пространственного распределения, (3) спрогнозировать возможные изменения ареала вида на фоне климатических изменений, (4) выявить рефугиумы с постоянно высокой вероятностью обнаружения вида, несмотря на климатические изменения. Мы использовали Maxent для моделирования современного и климатогенного ареалов *Fritillaria latifolia* с учетом абиотических переменных и антропогенных предикторов (расстояние до особо охраняемых природных территорий и пастбищ). Расстояния до антропогенной инфраструктуры рассчитывались с помощью показателя Path Distance, учитывающего горизонтальное расстояние по прямой, расстояние по поверхности и вертикальный фактор. Доступность территории (movement factor) формализовали через расстояние от оптимальных участков (с порогом пригодности местообитаний 0.8), на которых вероятность появления вида была выше 0.5. Наиболее важными абиотическими переменными в распределении видов были плювиотермический коэффициент Эмбергера, оптимальные значения которого соответствуют влажному и пергумидному климату, и индекс шероховатости рельефа с оптимальными значениями, варьирующими от почти ровных (81–116) до средне крутых (162–239) склонов. Расстояние до особо охраняемых природных территорий (0–1 км) было третьим значимым предиктором современного распространения *Fritillaria latifolia*, в то время как расстояние до пастбищ не внесло значительного вклада в модель. Расстояние пригодных территорий от оптимальных местообитаний (доступность территории) составило 15 км. Центры современного ареала вида локализованы на Западном и Центральном Кавказе, в Западном и Центральном Закавказье и на северо-западных хребтах Малого Кавказа в пределах сети особо охраняемых природных территорий, охватывающей большую часть высокогорий. Оптимистичный климатический сценарий SSP1-2.6 прогнозировал с 2021 по 2100 гг. уменьшение площади оптимальных для вида местообитаний в 1.6 раза, пессимистичный сценарий SSP5-8.5 – в 122 раза. Согласно климатическим моделям SSP1-2.6, к 2100 г. площадь рефугиумов составит 172.4 км^2 в высокогорных районах западной и центральной частей Большого Кавказа, включая территории Кавказского государственного природного биосферного заповедника и Тебердинского национального парка. Эти территории должны стать приоритетными для сохранения природных популяций *Fritillaria latifolia*.

Ключевые слова: Maxent, климатические сценарии, концепция Biotic-Abiotic-Movement, особо охраняемая природная территория, рефугиумы

REFERENCE SITES OF THREATENED RIVERINE ATLANTIC FOREST IN UPPER RIO DOCE WATERSHED

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The most important condition of ecological restoration is the identification of reference ecosystems, which function as a guide for assertive practice with which biological integrity and ecosystem structure and function can be compared. For restoration and conservation projects to be effective in the current scenario of biodiversity and ecosystem services decay worldwide, it is fundamental to understand the soil-plant interactions in each environment. In this study, we evaluated the structure and composition of the flora in 45 plots, equally distributed in three preserved areas (reference ecosystems) of Atlantic Forest in the upper Rio Doce watershed, Southeast Brazil. We also tested whether differences in species composition were influenced by edaphic factors, both in the adult tree and sapling strata. In both tree and sapling strata, Fabaceae was the species-richest family, followed by Myrtaceae, and Lauraceae. The Fabaceae family also showed the highest importance value for both strata. The soils of the riparian forests were highly heterogeneous among the studied sites. Co-inertia analyses indicated a clear edaphic-floristic gradient in both tree ($RV = 0.467$; $p < 0.001$) and sapling ($RV = 0.478$; $p < 0.001$) strata, with a connection of 46.7% and 47.8% between the edaphic and floristic matrices for trees and saplings, respectively. We identified the groups of tree and sapling strata species that were strongly associated with either nutritionally richer or poorer soils on each studied site. Understanding how ecological and life-history traits of plant species relate with edaphic factors is an important step to provide scientific-based knowledge to support policies for ecosystem recovery and restoration in the stretches of the Rio Doce watershed.

Key words: phytosociology, preserved forest, taxon-environment relationships, tree stratum, sapling stratum, vegetation structure

Introduction

Restoration is the process of recovering of an ecosystem that has been degraded, damaged, or destroyed (SER, 2004). This process initiates and/or accelerates the recovery of degraded areas, which premise is to re-arrange the complexity of biological assemblages, encompassing species composition and structure, and sustaining the biota of a given ecosystem over time (Suding et al., 2015; Rosenfield & Müller, 2017; Temperton et al., 2019). Given the current degradation of ecosystems all over the world, restoration actions are urgently needed and should focus on restoring ecosystem functionality and properties (e.g. Fernandes et al., 2016b; Kollmann et al., 2016; Gann et al., 2019).

The initiation of the restoration process must encompass the dissimilarities between current and expected future conditions in terms of composition, structure, and functions of the ecosystem (Laughlin, 2014). In this sense, one of the most important conditions of ecological restoration is the identification of reference ecosystems (Goebel et al., 2005; Toma et al., 2023). Reference ecosystems are defined as one or more existing, pre-existing, or hypothetical ecosystems that will serve as a reference template for restoration or mitigation projects (Hobbs & Harris, 2001; Miller & Hobbs, 2007; Miller et al., 2012; Toma et al., 2023). Reference ecosystems act as a guide for assertive practices and goals (Nestler et al., 2010; Temperton et al., 2019), from which biological integrity and ecosystem structure and function can be compared (Miller et al., 2012; Balaguer et al., 2014). The structure and composition of the plant community is the main factor responsible for creating and maintaining ecosystem functions and providing the basis for the development of other biotic communities (Whitham et al., 2006; De Deyn et al., 2008). Therefore, the evidence provided by reference ecosystems gives us the baselines to elucidate possible future trajectories and to measure the initiatives of ecological restoration success (Keenleyside et al., 2012; Higgs et al., 2014; Toma et al., 2023).

The characterisation of soil-plant interactions on reference ecosystems is of central importance for restoration and the effectiveness of conservation projects (e.g. Suding et al., 2015; Bauer et al., 2017). Soils play an important role in the diversity and functioning of tropical forests (Rodrigues et al., 2020; Bañares-de-Dios et al., 2022; Figueiredo et al., 2022; van der Sande et al., 2023), and a complex integrative system exists between soil formation and forest taxonomic composition, modulating patterns of niche differentiation on a global scale (Fujii et al., 2018). Soil nutrient availability shapes the distribution of tropical tree species, confirming the role of soils in plant community assembly as a mechanism for structuring these communities (John et al., 2007; Chadwick & Asner, 2018; Rodrigues et al., 2019; Lourenço et al., 2021; Figueiredo et al., 2022).

Understanding how soil factors modulate the structure of plant species composition and the underlying ecosystem processes is far from trivial. This is especially true for tropical forests that host more than half of the world's biodiversity and provide important ecosystem services for human survival (Lewis et al., 2015). The Brazilian Atlantic Forest is considered the 5th global biodiversity hotspot (Murray-Smith et al., 2009) with a high capacity of storing carbon (Magnago et al., 2015). However, it is one of the most threatened tropical forests in the world, mainly due to deforestation, which has generated an intense fragmentation process of this important ecosystem (Ribeiro et al., 2011a; Marques & Grelle, 2021). Additionally, we highlight the environmental disaster in the Rio Doce watershed, which caused the collapse of the Fundão dam in the municipality of Mariana (MG), southeast Brazil, in 2015. A tsunami of tailings caused the loss of approximately 14.69 km^2 of vegetation and 90% of the riparian vegetation of the River Fundão, River Gualaxo do Norte, and River Carmelo (Fernandes et al., 2016a; Bottino et al., 2017). The riparian habitats are considered Permanent Protected Areas under the Brazilian legislation (Metzger et al., 2019). This disaster caused numerous problems, affecting ecosystems and ecological interactions in this region (e.g. do Carmo et al., 2017; Sánchez et al., 2018). The wave of tailings released by the dam breach affected riparian habitats of the Atlantic Forest, leading to the loss of much of their regenerative capacity (Fernandes et al., 2016a). Therefore, it is of urgent importance to describe the interaction between edaphic factors and plant communities in reference ecosystems on the Rio Doce watershed in order to guide further restoration projects.

Our aim was to evaluate the structure and composition of the adult and sapling strata and its relationship with edaphic properties in the preserved areas (reference ecosystems) of the upper Rio Doce watershed. Our hypothesis was that small-scale edaphic heterogeneity plays an important role in shaping the species composition of adult and sapling strata. We expect this study to provide subsidies for the delimitation of a reference ecosystem that can be used in the planning of ecological restoration programmes in riparian forests, especially in the areas intensely affected after the environmental disaster of the collapse of the Fundão dam in Mariana municipality, in the upper Rio Doce watershed.

Material and Methods

Study site

To achieve our aims we sampled vegetation and soil in three old-growth riparian forests, located in the upper Rio Doce watershed, in Mariana municipality, Minas Gerais, southeastern Brazil (Fig. 1). The sampled sites are situated in three districts of the municipality of Mariana. Site 1: Santa Rita Durão district (20.276111° S, 43.430556° W) (Fig. S1a); Site 2: Monsenhor Horta district (20.304722° S, 43.219833° W) (Fig. S1b); Site 3: Camargos district (20.285361° S, 43.396806° W) (Fig. S1c). We selected reference sites for the study based on their state of conservation, prioritising sampling on accessible fragments that were in later stages of succession, and where the predominant physiognomy was an ombrophilous forest. According to the Köppen climate classification, the municipality of Mariana has a mesothermal climate (Cwa), with rainy summers and dry winters, average annual precipitation of 1571 mm and temperature ranging at 16.0–22.0°C, with an average value of 19.5°C (Alvares et al., 2013).

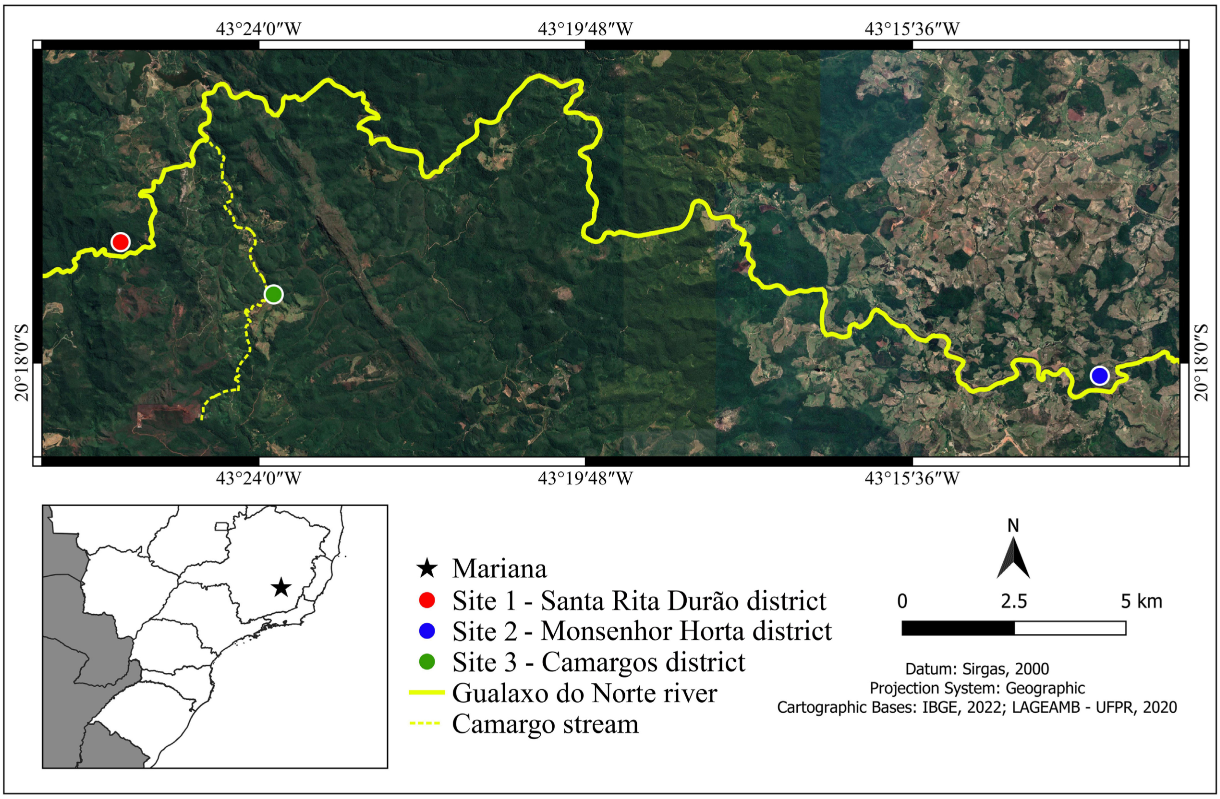

Fig. 1. Map showing the location of the three sampling sites in riparian forests in the upper Rio Doce watershed, Mariana municipality, Minas Gerais state, southeastern Brazil. Site 1 – Santa Rita Durão district; Site 2 – Monsenhor Horta district; Site 3 – Camargos district.

Vegetation sampling

We used the plot method to sample and characterise the reference ecosystem sites (Mueller-Dombois & Ellenberg, 1974). The phytosociological survey was conducted in 15 plots of 100 m^2 (10 × 10 m) at least 10 m apart from each other, totalling 45 plots (4500 m^2). We marked the plots with the aid of a level compass. To sample the tree stratum, we inventoried all tree individuals in each plot with DBH (diameter at breast height at 1.3 m from the ground) ≥ 5 cm. We marked all trees with aluminium plates in the trunk attached by nails and measured the circumference at breast height (CBH) using a tape measure (in cm). Samples of each plant individual were collected, identified with numbered adhesive tapes, and pressed to be later identified to the lowest possible taxonomic level. Because many individuals were not flowering at the sampling time, several further trips had to be made to the sites to collect fertile material for proper species identification.

Regarding the sampling of the sapling stratum, we allocated a 5 × 5 m sub-plot in the lower left corner (watercourse direction) within each 10 × 10 m plot. Within each sub-plot, with the aid of a digital caliper, we inventoried all herbaceous and shrubby individuals with DGH (diameter at ground height) between ≥ 1 and ≤ 5 cm. We marked all individuals within the sampling criteria with numbered aluminium plates, tied with nylon thread, and measured the height of each individual with the aid of a wooden tape measure (Menino et al., 2009, 2012).

We collected plant material (vegetative or reproductive) for identification with specialised literature and existing material, and to make exsiccates. After this step, we deposited all identified specimens in the Montes Claros Herbarium (MCMG) at the State University of Montes Claros (Unimontes). The family names followed the Angiosperm Phylogeny Group (APG IV, 2016). Synonymy verification, nomenclature and species authors were obtained through the «WorldFlora» package (Kindt, 2020) in the R environment (R Core Team, 2018), standardised according to World Flora Online (https://www.worldfloraonline.org/). We made additional checks with the Flora e Funga do Brasil (2022) for species, which were not found in World Flora Online. The parameters calculated for the vegetation phytosociology were the absolute and relative values of density, dominance, frequency, and importance value (IV) (Mueller-Dombois & Ellenberg, 1974).

Soil sampling

We collected about 100 g of simple soil samples at 20 cm depth at the four corners of each plot and at its centre. These were mixed *in situ* and transformed into a composite sample per plot, totaling 45 soil samples for the study. Each composite sample represented a valid estimate of the mean edaphic parameters for the plot (Binkley & Vitousek, 1989). We collected the soil samples according to the procedures described in Dick et al. (1996), where each sample was dried in the shade, kept at room temperature, crushed, completely homogenised, and identified, and then sent for chemical and granulometric analysis by the Soil Department of the Federal University of Viçosa (UFV). All soil granulometric analyses (coarse sand, fine sand, silt, and clay fractions) followed the protocol proposed by Donagemma et al. (2017). The measurement of pH in water used 1.0 : 2.5 (v/v) soil : solution ratios. The exchangeable Ca^{2+}, Mg^{2+}, and Al^{3+} cations were extracted by 1 mol/L KCl solution, and the Ca^{2+} and Mg^{2+} contents were determined in the extract by titration with EDTA 0.01 mol/L and the Al^{3+} contents by titration with NaOH 0.025 mol/L, according to Silva et al. (1999). The elements P and K were extracted by Mehlich 1 solution, and the levels of these elements in the extracts were determined by spectrophotometry, according to Silva et al. (1999). Potential acidity (H + Al) was extracted by 0.5 mol/L calcium acetate solution at pH 7.0 and determined by alkalimetric titration of the extract (Silva et al., 1999). The base saturation and aluminium saturation were calculated, respectively as follows (see Alvarez Venegas et al., 1999):

$$\text{Base saturation} = 100 \times \frac{K + Ca^{2+} + Mg^{2+}}{K + Ca^{2+} + Mg^{2+} + H + Al}$$

$$\text{Aluminium saturation} = 100 \times \frac{Al}{K + Ca^{2+} + Mg^{2+} + Al^{3+}}$$

Data analyses

To access the sufficiency of the sampling efforts, we constructed rarefaction curves for species diversity using the function «rare_Rao» from package «adiv» (Pavoine, 2020) in the R environment (R Core Team, 2018) following Ricotta et al. (2012), in which expected species diversity for each sampling site was computed as a function of the cumulative number of plots. We used the resampling approach with 10 000 iterations. We evaluated the pattern of exclusive and shared species among the three studied sites through Venn diagrams constructed for both tree and sapling stratum using the package «VennDiagram» (Chen & Boutros, 2011) in the R environment (R Core Team, 2018).

To compare the mean values of each edaphic factor between sites, we used ANOVA followed by post-hoc pairwise Tuckey tests. We tested the normality of ANOVA residuals using the Shapiro-Wilk test, and when the residuals were non-normal, we used the Kruskal-Wallis followed by post-hoc pairwise Mann-Whitney tests (Quinn & Keough, 2002). To determine the relationships between the edaphic variables and the plant species community, we used the co-inertia analysis. This analysis is a general and flexible method that measures the concordance (also called co-structure) between two multivariate data sets (Dolédec & Chessel, 1994; Dray et al., 2003). We applied the co-inertia analysis to quantify and test the association between two matrices simultaneously. We defined the edaphic matrix as the mean values of 13 edaphic factors across the 45 plots, while the floristic matrix consisted of the incidence (presence and absence) of 174 tree species and 189 sapling species across the 45 plots. The co-inertia analysis results in a value called «RV», which measures the strength of association between the two matrices. The RV value is limited to 0 (i.e. no association) and 1 (i.e. maximum association). We accessed the significance of the co-inertia (p-value) by Monte Carlo permutation, performed with 10 000 randomisations. To implement the co-inertia, we used a standardised and centred PCA (mean = 0; standard deviation = 1) for the edaphic matrix, and a centred PCA (mean = 0) for the floristic matrix, according to Dray et al. (2003). To achieve the assumptions of normality in the edaphic data, we used the square root transformation for magnesium (Mg), aluminium (Al), base saturation, and fine sand content. In addition, we used logarithmic transformation for phosphorus (P), calcium (Ca), and clay contents. We performed the co-inertia analysis in the R environment (R Core Team, 2018) using the package «ade4» (Dray & Dufour, 2007). To evaluate the association between each edaphic variable and the co-ordinates of the plots on axis 1 of co-inertia, we used Pearson's correlation, while we defined the association between species and axis 1 of co-inertia by the co-ordinates of the species on this axis (Pavoine et al., 2011).

Results

In this study, we recorded 291 plant species belonging to 49 families, of which 174 species of 45 families at the tree stratum (Table S1), and 189 species of 40 families at the sapling stratum (Table S2). The rarefaction curves shown in Fig. 2 indicate a sufficient sampling of species diversity for the three sites of both tree (Fig. 2a,b,c) and sapling stratum (Fig. 2d,e,f) since the expected species diversity showed a trend for stabilisation.

At the tree stratum, the richest families were Fabaceae (26 species), followed by Myrtaceae (18 species), Lauraceae (12 species), and Melastomataceae (8 species). Twenty families were represented by only one species (Table S1). Regarding the importance value (IV), Fabaceae accounted for 21.3% of IV, followed by Lauraceae (9.2%), Myrtaceae (8.9%), and Sapindaceae (7.4%) (Table S1). The most important tree species was *Hieronyma alchorneoides* Allemão (Phyllanthaceae; IV = 5.8%), followed by *Nectandra megapotamica* (Spreng.) Mez (Lauraceae; IV = 4.0%), *Siparuna guianensis* Aubl. (Siparunaceae; IV = 4.0%), and *Cupania vernalis* Cambess. (Sapindaceae; IV = 3.2%) (Table S1). At the tree stratum 19 taxa could not be identified and these unidentified species accounted for 5.2% of IV.

At the sapling stratum, the richest families were Fabaceae (23 species), followed by Myrtaceae (21 species), Lauraceae (12 species), and Rubiaceae (11 species). Fifteen families were represented by only one species (Table S2). Regarding the IV, the family Fabaceae accounted for 18.2% of IV, followed by Siparunaceae (IV = 11.6%), Rubiaceae (IV = 9.8%), and Myrtaceae (IV = 9.5%) (Table S2). The most important sapling species was *Dalbergia nigra* (Vell.) Allemão ex Benth. (Fabaceae; IV = 11.4%), followed by *Siparuna guianensis* (IV = 7.0%), *S. reginae* (Tul.) A.DC. (Siparunaceae; IV = 4.5%), and *Psychotria vellosiana* Benth. (Rubiaceae; IV = 3.8%) (Table S2). At the sapling stratum, 21 taxa were not identified and these unidentified species accounted for 4.5% of IV.

Ten species from the tree stratum occurred on all three studied sites, namely *Aniba firmula* Mez (Lauraceae), *Annona sylvatica* A.St.-Hil. (Annonaceae), *Dalbergia nigra*, *Guatteria villosissima* A.St.-Hil. (Annonaceae), *Machaerium hirtum* (Vell.) Stellfeld (Fabaceae), *Nectandra oppositifolia* Nees & Mart. (Lauraceae), *Platypodium elegans* Vogel (Fabaceae), *Senna multijuga* (Rich.) H.S.Irwin & Barneby (Fabaceae), *Siparuna guianensis*, and *Xylopia sericea* A.St.-Hil. (Annonaceae) (Fig. 3a). Among these species, only *Platypodium elegans* stands among the ten most important species from the tree stratum. Most species occurred exclusively on just one site. The number of exclusive tree species on site 1, 2, and 3 were, respectively, 73 (74%), 29 (58%), and 43 (67%) (Fig. 3a). Regarding the sapling stratum, six species occurred on all three studied sites, *Cestrum axillare* Vell. (Solanaceae), *Dalbergia nigra*, *Guatteria villosissima*, *Nectandra oppositifolia*, *Siparuna reginae*, and *Xylopia sericea* (Fig. 3b). With the exception of *Guatteria villosissima* and *Xylopia sericea*, these species stand among the ten most important species of the sapling stratum (Table S2). Similar to the tree stratum, the majority of sapling species were exclusive for one site. The number of exclusive sapling species on site 1, 2, and 3 were, respectively, 64 (67%), 51 (72%), and 39 (62%) (Fig. 3b).

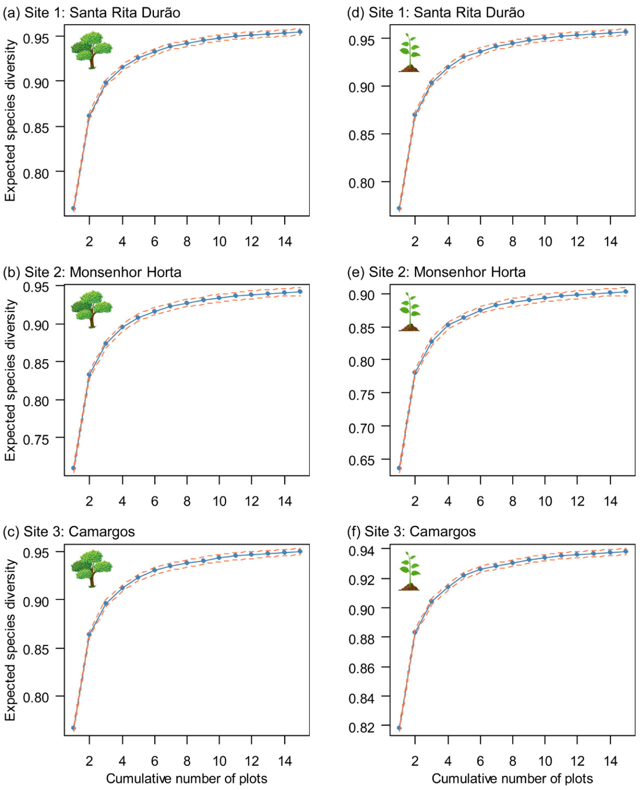

Fig. 2. Rarefaction curves for species diversity (Gini-Simpson index) as a function of sampling effort (cumulative number of plots) on three sampling sites of riparian forests in the upper Rio Doce watershed, Mariana, Minas Gerais, southeastern Brazil. Designations: a, b, c – tree stratum on sites 1, 2, 3, respectively; d, e, f – sapling stratum on sites 1, 2, 3, respectively. Blue dots and continuous line indicate the expected species diversity; red dashed line indicates the 95% confidence interval. The districts of each site are indicated.

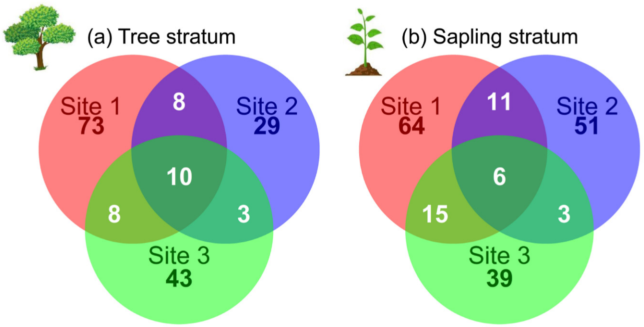

Fig. 3. Venn diagram illustrating the exclusive and shared species among three studied sites from tree (a) and sapling (b) strata of riparian forests in the upper Rio Doce watershed, Mariana municipality, Minas Gerais state, southeastern Brazil. Designations: Site 1 – Santa Rita Durão district; Site 2 – Monsenhor Horta district; Site 3 – Camargos district.

The soils of the studied riparian forests showed a considerable variation that indicates a high heterogeneity among the sites (Table 1). According to the soil chemical properties, the pH ranged from highly acidic (3.6) to mildly acidic (6.1), while the aluminium saturation ranged from 0.0% to 90.1%. The base saturation ranged from 1.7% to 67.1%, the content of calcium ranged from 0.0 $cmol_c/dm^3$ to 4.0 $cmol_c/dm^3$, and the content of phosphorus ranged from 0.9 mg/dm^3 to 7.6 mg/dm^3. Regarding the soil texture, there was also a wide variation among the sampling plots (Table 1). The proportion of fine sand ranged from 5.7% to 69.0%, while the proportion of clay ranged from 7.0% to 54.5%. The comparison among sites indicated that there were significant differences among sites for all edaphic factors analysed (Table 1). The soil from site 3 (Camargos district) was significantly more acidic, and less fertile, with a higher aluminium concentration, while the soil from site 1 (Santa Rita Durão district) showed the opposite pattern, with less acidic, more fertile, and had a lower aluminium concentration (Table 1).

The co-inertia analysis (COIA) evidenced a clear edaphic-floristic gradient at both tree and sapling strata. The overall association between tree species and edaphic parameters was highly significant (RV = 0.467; $p < 0.001$) according to the COIA (Monte Carlo with 10 000 permutations). We found a connection of 46.7% between the edaphic and tree floristic matrices. The percentage of covariance explained by the tree stratum COIA axis 1 was 83.7%, while axis 2 explained 10.0% of the covariance. Thus, we further explored only the COIA axis 1. The positive side of the COIA axis 1 showed plots with nutritionally rich and less acidic soils, a higher content of calcium and magnesium, and a higher proportion of fine sand (Fig. 4a). Tree species more strongly associated with the positive side of this axis were *Nectandra megapotamica*, *Schinus terebinthifolia* Raddi (Anacardiaceae), *Guarea guidonia* (L.) Sleumer (Meliaceae), *Eugenia florida* DC. (Myrtaceae), *Syzygium jambos* (L.) Alston (Myrtaceae), and *Dendropanax cuneatus* Decne. & Planch. (Araliaceae) (Fig. 4b). On the other hand, the negative side of COIA axis 1 showed plots with acidic and nutritionally poor soils, with a higher aluminium saturation, a higher content of aluminium, potential acidity (H + Al), phosphorus, and a higher proportion of clay and coarse sand (Fig. 4a). Tree species more strongly associated with the negative side of this axis were *Erythroxylum pelleterianum* A.St.-Hil. (Erythroxylaceae), *Cupania vernalis*, *Piptadenia gonoacantha* (Mart.) J.F.Macbr. (Fabaceae), *Moquiniastrum paniculatum* (Less.) G.Sancho (Asteraceae), *Myrcia guianensis* DC., *M. retorta* Cambess. (Myrtaceae), and *Nectandra oppositifolia* (Fig. 4b).

Table 1. Soil parameters for each sampling site (N = 15 plots per site) in riparian forests in the upper Rio Doce whatershed, Mariana, Minas Gerais, southeastern Brazil

Site	Site 1 Santa Rita Durão M ± SE	Site 2 Monsenhor Horta M ± SE	Site 3 Camargos M ± SE	Statistics (p-value)
pH (H_2O)	5.23 ± 0.12^a	4.61 ± 0.07^b	3.88 ± 0.05^c	F = 66.12 ($p < 0.001$)
P (mg/dm^3)	2.36 ± 0.19^a	2.41 ± 0.22^a	4.19 ± 0.42^b	F = 9.52 ($p < 0.001$)
K (mg/dm^3)	51.19 ± 3.39^a	29.72 ± 3.26^b	54.40 ± 2.03^a	F = 20.64 ($p < 0.001$)
Ca ($cmol_c/dm^3$)	1.99 ± 0.24^a	0.89 ± 0.07^b	0.33 ± 0.19^c	H = 27.76 ($p < 0.001$)
Mg ($cmol_c/dm^3$)	0.87 ± 0.07^a	0.38 ± 0.03^b	0.28 ± 0.07^c	H = 25.10 ($p < 0.001$)
Al ($cmol_c/dm^3$)	0.12 ± 0.04^a	0.59 ± 0.06^b	1.85 ± 0.09^c	F = 167.80 ($p < 0.001$)
H+Al ($cmol_c/dm^3$)	4.34 ± 0.55^a	5.00 ± 0.67^a	11.55 ± 0.32^b	H = 26.97 ($p < 0.001$)
Base saturation (%)	42.79 ± 4.31^a	24.13 ± 2.88^b	5.74 ± 1.70^c	F = 48.58 ($p < 0.001$)
Al saturation (%)	5.64 ± 2.56^a	31.00 ± 2.93^b	75.95 ± 5.15^c	H = 33.93 ($p < 0.001$)
Coarse sand (%)	10.27 ± 1.56^a	14.11 ± 1.95^{ab}	19.97 ± 1.91^b	F = 7.27 ($p < 0.01$)
Fine sand (%)	38.33 ± 3.12^a	41.48 ± 3.22^a	17.37 ± 1.53^b	H = 28.80 ($p < 0.001$)
Silt (%)	33.80 ± 2.24^a	25.95 ± 2.87^a	17.08 ± 2.06^b	F = 12.02 ($p < 0.001$)
Clay (%)	17.60 ± 1.32^a	18.48 ± 1.68^a	45.58 ± 1.39^b	H = 29.42 ($p < 0.001$)

Note: M – mean value, SE – standard error. Districts of each site are indicated. Lowercase letters denote significant differences ($p < 0.05$) according to ANOVA (F) followed by the post-hoc Tuckey pairwise test, or Kruskal-Wallis (H) followed by the Mann-Whitney pairwise test when residuals of ANOVA were not normal.

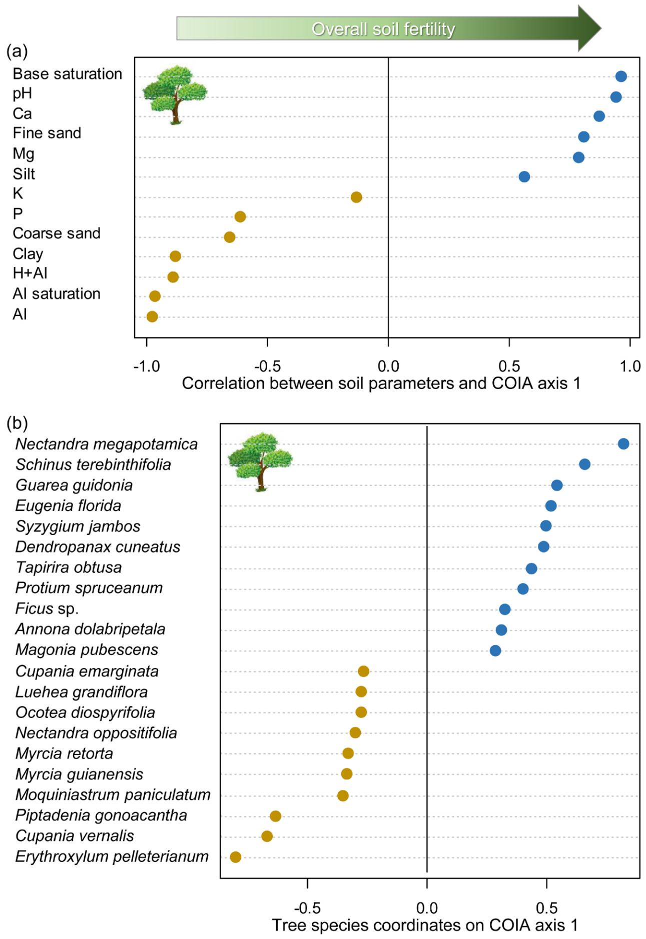

Fig. 4. Co-structure between edaphic parameters and tree species community sampled on three sites from riparian forests in the upper Rio Doce watershed, Mariana municipality, Minas Gerais state, southeastern Brazil. Designations: (a) – Pearson's correlation between edaphic factors and plot co-ordinates on co-inertia analysis (COIA) axis 1; (b) – co-ordinates of tree species with highest association with positive and negative side of COIA axis 1. The green arrow at the top indicates the overall direction of the soil fertility gradient. Orange and blue circles represent, respectively, negative and positive values of correlation (a) or co-ordinates (b) on COIA axis 1.

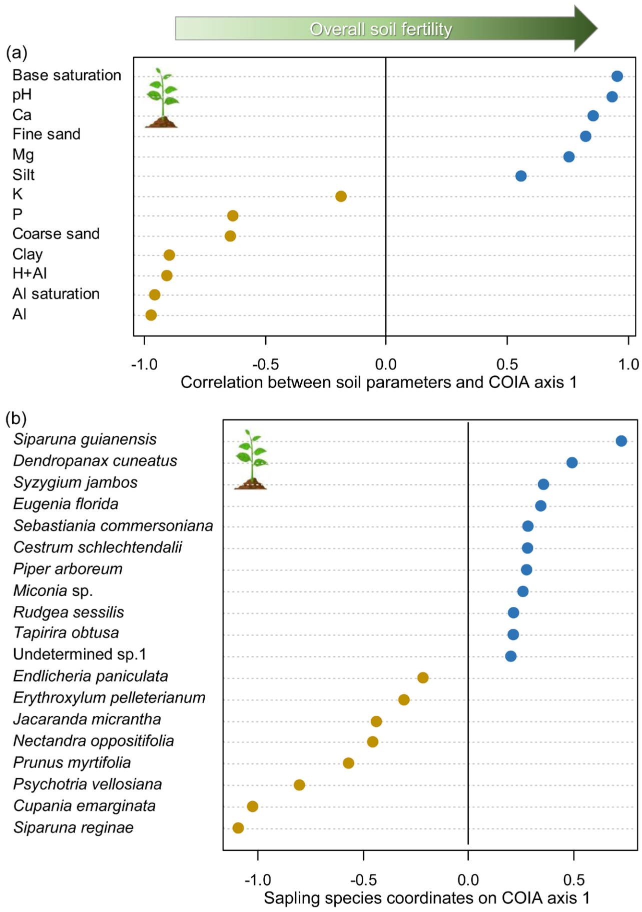

Fig. 5. Co-structure between edaphic parameters and sapling species community sampled on three sites from riparian forests in the upper Rio Doce watershed, Mariana municipality, Minas Gerais state, southeastern Brazil. Designations: (a) – Pearson's correlation between edaphic factors and plot co-ordinates on co-inertia analysis (COIA) axis 1; (b) – co-ordinates of sapling species with the highest association with positive and negative side of COIA axis 1. The green arrow at the top indicates the overall direction of the soil fertility gradient. Orange and blue circles represent, respectively, negative and positive values of correlation (a) or co-ordinates (b) on COIA axis 1.

Regarding the sapling stratum, the overall association between sapling species and edaphic parameters was also highly significant (RV = 0.478; $p < 0.001$) according to the COIA (Monte Carlo with 10 000 permutations). We found a connection of 47.8% between the edaphic and sapling floristic matrices. The percentage of covariance explained by COIA axis 1 was 82.4%, while axis 2 explained 10.7% of the covariance. Thus, similar to the COIA based on the tree stratum, we further explored only the COIA axis 1 for the sapling stratum. The positive side of the sapling-based COIA axis 1 evidenced a very similar pattern to the tree-based COIA, showing plots with nutritionally rich and less acidic soils, with a higher content of calcium and magnesium and a higher proportion of fine sand (Fig. 5a). Sapling species more strongly associated with the positive side of this axis were: *Siparuna guianensis*, *Dendropanax cuneatus*, *Syzygium jambos*, *Eugenia florida*, *Sebastiania commersoniana* (Baill.) L.B.Sm. & Downs (Euphorbiaceae), and *Cestrum schlechtendalii* G.Don (Solanaceae) (Fig. 5b). On the other hand, likewise the tree stratum COIA, the negative side of sapling-based COIA axis 1 showed plots with acidic and nutritionally poor soils, a higher aluminium saturation, a higher content of aluminium, phosphorus, and a higher proportion of clay and coarse sand (Fig. 5a). Sapling species more strongly associated with the negative side of this axis were: *Siparuna reginae*, *Cupania emarginata* Cambess. (Sapindaceae), *Psychotria vellosiana*, *Prunus myrtifolia* (L.) Urb. (Rosaceae), *Nectan-*

dra oppositifolia, and *Jacaranda micrantha* Cham. (Bignoniaceae) (Fig. 5b).

Discussion

Understanding the processes that drive biodiversity in natural environments is essential for creating effective policies that ensure the success of restoration projects. Phytosociological studies integrated with edaphic factors surveys stand out for their high importance, as they allow the comparison across various sites with varied situations of the same ecosystem. As a result, we may be able to identify the agents or factors that boost the recovery of the environment and assist in the definition of mitigating measures (Balestrin et al., 2019). Furthermore, these studies are indispensable in the process of establishing reference ecosystems, a crucial step in the restoration process, because this information allows us to set goals and to monitor the success of the restoration (Turchetto et al., 2017; Durbecq et al., 2020; Toma et al., 2023). In the present case, scientific knowledge about the reference ecosystem for the proper restoration of the riverine forests in the Rio Doce watershed is fundamental and urgent because many initiatives are being implemented, unfortunately without understanding the native vegetation of the riparian ecosystems.

Our phytosociological data showed a high floristic diversity, in which 820 individuals of in total 291 species were sampled in the tree stratum, and 899 individuals belonging to 189 species were sampled in the sapling stratum. The number of species reflects the high floristic diversity found in the Atlantic Forest, shaped by local environmental conditions, such as variation in soil quality (Fagundes et al., 2019; Figueiredo et al., 2022) and successional stages (Forzza et al., 2012). Here, we found a predominance of species from the Fabaceae and Myrtaceae families, corroborating previous floristic surveys conducted at various regions of the Atlantic Forest (Oliveira et al., 2011; Miranda et al., 2019; Dias et al., 2021). These families are important indicators of community development (Tabarelli et al., 1994; Gei et al., 2018). Some species from the Myrtaceae family are indicators of the forest quality, where degraded habitats tend to have lower species richness of this family (Amorim et al., 2009; Rigueira et al., 2013). The Fabaceae family is widely distributed in the Neotropical forests and many species are nitrogen-fixing, contributing to a greater availability of this nutrient in the ecosystem (Gei et al., 2018).

Among all species sampled in the sapling stratum, *Dalbergia nigra* stood out by presenting the highest importance value. This species has a distribution restricted to the Atlantic Forest (Silva Júnior et al., 2022), and is known for its economic and ecological potential (Carvalho, 1994). Due to the overexploitation of *Dalbergia nigra* populations and anthropic impacts on its natural habitat (Ribeiro et al., 2011b), this species is classified as Vulnerable in relation to the risk of extinction (Varty, 1998). This pioneer species is classified as evergreen to semideciduous and occurs on well-drained slopes, as well as inside dense primary forests and in secondary formations (Lorenzi, 1992). *Dalbergia nigra* produces a high abundance of seeds, allowing it to colonise a wide variety of environments. These ecological traits make *Dalbergia nigra* a species with great potential for mitigation projects or in the recovery of degraded environment, besides influencing the nutritional factors of the soil due to its nitrogen-fixing capability (Silva Júnior et al., 2020).

The species with the highest IV for both tree and sapling stratum are predominantly composed of species with zoochoric dispersal. For example, in the sapling stratum, *Siparuna guianensis* and *S. reginae* are respectively the second and third most important species in the studied riparian forests. *Siparuna guianensis* has fruits dispersed mainly by ants, birds, and mammals (Oliveira & Paula, 2001; Magalhães et al., 2018), and *Siparuna reginae* has also a zoochoric dispersal (Armando et al., 2011). The association of these species with animals helps to promote the recovery of ecosystem services and favours the structuring of these environments. The recurrence of species with zoochoric dispersal is a pattern commonly found in other studies in the Atlantic Forest (Oliveira et al., 2011; Suganuma et al., 2013; Franco et al., 2014). Plant species dispersed by animals can accelerate the successional process, facilitating the recovery of ecosystems (Sansevero et al., 2011). The local fauna is an important driver of the spatial distribution of vegetation in forest ecosystems (Negrini et al., 2012; Franco et al., 2014) increasing the genetic variability of species (Almeida et al., 2008). Limiting factors that affect dispersal simplify species composition, where closer communities tend to have similar composition, even without taking into account ecological similarity (Beaudrot et al., 2013).

Our data support the importance of soil characteristics in modulating the structure of plant species composition in tropical forests (e.g. Veloso et al., 2014; Coelho et al., 2018; Fagundes et al., 2019; Figueiredo et al., 2022; van der Sande et al., 2023). We found congeneric species associated with opposite conditions of the edaphic gradient, both in the tree and sapling stratum. In the sapling stratum *Siparuna guianensis* was associated with less acidic, nutritionally richer soils with a higher proportion of fine sand. On the other hand, *Siparuna reginae* was associated with more acid soils, nutritionally poor, and a higher proportion of clay. Therefore, we emphasise that the results found here should not be extrapolated to other taxonomically close species, because in many cases species of the same genus may respond in contrasting ways to the characteristics of each location, as shown here. Similarly, the congeneric pair of the tree stratum, *Nectandra megapotamica* and *N. oppositifolia*, were associated with opposite edaphic gradient conditions. *Nectandra megapotamica* was associated with less acidic and nutritionally richer soils. This species is classified as late secondary, shade tolerant, and strongly associated with moist soils (Lorenzi, 1998). On the other hand, *Nectandra oppositifolia* was associated with more acidic soils, nutritionally poor, and with a higher proportion of clay. *Nectandra oppositifolia* has a rapid growth in both the early and secondary stage, and its fruits are dispersed by birds (Gandolfi et al., 1995). Pioneer species that dominate early succession stages are fundamental in facilitating processes, helping plant community re-composition (Kong et al., 2023). Thus, *Nectandra oppositifolia* potentially plays an important role in the recruitment of species in areas with relatively more restrictive edaphic characteristics.

Conclusions

Understanding how ecological and life-history traits of plant species, such as dispersal mechanisms and growth relate to edaphic factors is an important step to providing scientific-based knowledge to support policies for ecosystem recovery and restoration (Garnier et al., 2004; Kattge et al., 2011). We emphasise that studies of this nature must be conducted in various regions of the Atlantic Forest to broaden our knowledge about the association patterns between plant species and soil characteristics of this mega-diverse ecosystem. These patterns of association are extremely important because of modifying patterns of richness and act on species composition, showing that each type of habitat needs specific conservation plans for the ecosystem. Our results provide a solid attempt to generate information for reference ecosystems in the Rio Doce watershed, southeast Brazil, a region subjected to large-scale human disturbances that need urgent restoration practice.

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Supporting Information

Additional data for the paper of Figueiredo et al. (2024) may be found in the **Supporting Information**.

References

Almeida S.R., Watzlawick L.F., Myszka E., Valerio A.F. 2008. Florística e síndromes de dispersão de um remanescente de Floresta Ombrófila Mista em sistema faxinal. *Ambiência* 4(2): 289–297.

Alvares C.A., Stape J.L., Sentelhas P.C., Moraes Gonçalves J.D., Sparovek G. 2013. Köppen's climate classification map for Brazil. *Meteorol Zeitschrift* 22(6): 711–728. DOI: 10.1127/0941-2948/2013/0507

Alvarez Venegas V.H., Novais R.F., Barros N.F., Cantarutti R.B., Lopes A.S. 1999. Interpretação dos resultados das análises de solos. In: A.C. Ribeiro, P.T.G. Guimarães, V.H. Alvarez Venegas (Eds.): *Recomendações para o uso de corretivos e fertilizantes em Minas Gerais*. Viçosa, Brazil: CFSEMG. P. 25–32.

Amorim A.M., Jardim J.G., Lopes M.M.M., Fiaschi P., Borges R.A.X., Perdiz R.O., Thomas W.W. 2009. Angiospermas em remanescentes de floresta montana no sul da Bahia, Brasil. *Biota Neotropica* 9(3): 313–348. DOI: 10.1590/S1676-06032009000300028

APG IV. 2016. An update of Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* 181(1): 1–20. DOI: 10.1111/boj.12385

Armando D.M.S., Rosa T.C., Sousa H., Silva R.A., Silva Carvalho L.C., Gonzaga A.P.D., Machado E.L.M., Costa M.P. 2011. Colonização de espécies arbustivo-arbóreas em povoamento de *Eucalyptus* spp., Lavras, MG. *Floresta Ambiente* 18(4): 376–389. DOI: 10.4322/floram.2011.057

Balaguer L., Escudero A., Martín-Duque J.F., Mola I., Aronson J. 2014. The historical reference in restoration ecology: Re-defining a cornerstone concept. *Biological Conservation* 176: 12–20. DOI: 10.1016/j.biocon.2014.05.007

Balestrin D., Martins S.V., Schoorl J.M., Lopes A.T., de Andrade C.F. 2019. Phytosociological study to define restoration measures in a mined area in Minas Gerais, Brazil. *Ecological Engineering* 135: 8–16. DOI: 10.1016/j.ecoleng.2019.04.023

Bañares-de-Dios G., Macía M.J., de Carvalho G.M., Arellano G., Cayuela L. 2022. Soil and climate drive floristic composition in tropical forests: A literature review. *Frontiers in Ecology and Evolution* 10: 866905. DOI: 10.3389/fevo.2022.866905

Bauer J.T., Blumenthal N., Miller A.J., Ferguson J.K., Reynolds H.L. 2017. Effects of between-site variation in soil microbial communities and plant-soil feedbacks on the productivity and composition of plant communities. *Journal of Applied Ecology* 54(4): 1028–1039. DOI: 10.1111/1365-2664.12937

Beaudrot L., Rejmánek M., Marshall A.J. 2013. Dispersal modes affect tropical forest assembly across trophic levels. *Ecography* 36(9): 984–993. DOI: 10.1111/j.1600-0587.2013.00122.x

Binkley D., Vitousek P. 1989. Soil nutrient availability. In: R.W. Pearcy, J.R. Ehleringer, H.A. Mooney, P.W. Rundel (Eds.): *Plant Physiological Ecology: Field Methods and Instrumentation*. London, UK: Kluwer Academic Publishers. P. 75–96. DOI: 10.1007/978-94-009-2221-1_5

Bottino F., Milan J.A.M., Cunha-Santino M.B., Bianchini I. 2017. Influence of the residue from an iron mining dam in the growth of two macrophyte species. *Chemosphere* 186: 488–494. DOI: 10.1016/j.chemosphere.2017.08.030

Carvalho P.E.R. 1994. *Espécies florestais brasileiras: Recomendações silviculturais, potencialidades e uso da madeira*. Colombo: EMBRAPA-CNPF. 640 p.

Chadwick K.D., Asner G.P. 2018. Landscape evolution and nutrient rejuvenation reflected in Amazon forest canopy chemistry. *Ecology Letters* 21(7): 978–988. DOI: 10.1111/ele.12963

Chen H., Boutros P.C. 2011. VennDiagram: a package for the generation of highly-customizable Venn and Euler diagrams in R. *BMC Bioinformatics* 12: 35. DOI: 10.1186/1471-2105-12-35

Coelho M.S., Carlos P.P., Pinto V.D., Meireles A., Negreiros D., Morellato L.P.C., Fernandes G.W. 2018. Connection between tree functional traits and environmental parameters in an archipelago of montane forests surrounded by rupestrian grasslands. *Flora* 238: 51–59. DOI: 10.1016/j.flora.2017.04.003

De Deyn G.B., Cornelissen J.H.C., Bardgett R.D. 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology Letters* 11(5): 516–531. DOI: 10.1111/j.1461-0248.2008.01164.x

Dias P.B., Gomes L.P., Callegaro R.M., Carvalho F.A., Dias H.M. 2021. Structural and environmental variability from the edge to the interior of an Atlantic Forest remnant in Brazil. *Journal of Tropical Forest Science* 33(3): 308–322. DOI: 10.26525/jtfs2021.33.3.308

Dick R.P., Thomas D.R., Halvorson J.J. 1996. Standardized methods, sampling, and sample pretreatment. In: J.W. Doran, A.J. Jones (Eds.): *Methods for assessing soil quality*. Vol. 49. Madison, USA: SSSA. P. 107–121. DOI: 10.2136/sssaspecpub49.c6

do Carmo F.F., Kamino L.H.Y., Tobias Junior R., de Campos I.C., do Carmo F.F., Silvino G., de Castro K.J.S.X., Mauro M.L., Rodrigues N.U.A., Miranda M.P.S., Pinto C.E.F. 2017. Fundão tailings dam failures: the environment tragedy of the largest technological disaster of Brazilian mining in global context. *Perspectives in Ecology and Conservation* 15(3): 145–151. DOI: 10.1016/j.pecon.2017.06.002

Dolédec S., Chessel D. 1994. Co-inertia analysis: an alternative method for studying species-environment relationships. *Freshwater Biology* 31(3): 277–294. DOI: 10.1111/j.1365-2427.1994.tb01741.x

Donagemma G.K., Viana J.H.M., Almeida B.G., Ruiz H.A., Klein V.A., Dechen S.C.F., Fernandes R.B.A. 2017. Análise granulométrica. In: P.C. Teixeira, G.K. Donagemma, A. Fontana, W.G. Teixeira (Eds.): *Manual de métodos de análise de solo*. 3 ed. Brasília: Embrapa Solos. P. 95–116.

Dray S., Dufour A.B. 2007. The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software* 22(4): 1–20. DOI: 10.18637/jss.v022.i04

Dray S., Chessel D., Thioulouse J. 2003. Co-inertia analysis and the linking of ecological data tables. *Ecology* 84(11): 3078–3089. DOI: 10.1890/03-0178

Durbecq A., Jaunatre R., Buisson E., Cluchier A., Bischoff A. 2020. Identifying reference communities in ecological restoration: the use of environmental conditions driving vegetation composition. *Restoration Ecology* 28(6): 1445–1453. DOI: 10.1111/rec.13232

Fagundes N.C.A., Ávila M.A., Souza S.R., Azevedo I.F.P., Nunes Y.R.F., Fernandes G.W., Fernandes L.A., dos Santos R.M., Veloso M.D.M. 2019. Riparian vegetation structure and soil variables in Pandeiros river, Brazil. *Rodriguésia* 70: e01822017. DOI: 10.1590/2175-7860201970002

Fernandes G.W., Goulart F.F., Ranieri B.D., Coelho M.S., Dales K., Boesche N., Bustamante M., Carvalho F.A., Carvalho D.C., Dirzo R., Fernandes S., Galetti P.M., Millan V.E.G., Milke C., Ramirez J.L., Neves A., Rogass C., Ribeiro S.P., Scariot A., Soares-Filho B. 2016a. Deep into the mud: ecological and socioeconomic impacts of the dam breach in Mariana, Brazil. *Natureza & Conservação* 14(2): 35–45. DOI: 10.1016/j.ncon.2016.10.003

Fernandes G.W., Toma T.S.P., Angrisano P., Overbeck G. 2016b. Challenges in the restoration of quartzitic and ironstone rupestrian grasslands. In: G.W. Fernandes (Ed.): *Ecology and conservation of mountaintop grasslands in Brazil*. Switzerland: Springer. P. 449–477. DOI: 10.1007/978-3-319-29808-5_19

Figueiredo J.C.G., de Ávila M.A., Souza C.S., Neves J.G.S., Tolentino G.S., Oki Y., Azevedo I.F.P., Negreiros D., Viana J.H.M., dos Santos R.M., Fonseca R.S., Fernandes G.W., Nunes Y.R.F. 2022. Relationship of woody species composition with edaphic characteristics in threatened riparian Atlantic Forest remnants in the upper Rio Doce basin, Brazil. *Nordic Journal of Botany* 2022(11): e03679. DOI: 10.1111/njb.03679

Flora e Funga do Brasil. 2022. Jardim Botânico do Rio de Janeiro. Available from https://floradobrasil.jbrj.gov.br/

Forzza R.C., Baumgratz J.F.A., Bicudo C.E.M., Canhos D.A.L., Carvalho A.A., Coelho M.A.N., Costa A.F., Costa D.P., Hopkins M.G., Leitman P.M., Lohmann L.G., Lughadha E.N., Maia L.C., Martinelli G., Menezes M., Morim M.P., Peixoto A.L., Pirani J.R., Prado J., Queiroz L.P., Souza S., Souza C.V., Stehmann J.R., Sylvestre L.S., Walter B.M.T., Zappi D.C. 2012. New Brazilian floristic list highlights conservation challenges. *BioScience* 62(1): 39–45. DOI: 10.1525/bio.2012.62.1.8

Franco B.K.S., Martins S.V., Faria P.C.L., Ribeiro G.A., Neto A.M. 2014. Estrato de regeneração natural de um trecho de floresta estacional semidecidual, Viçosa, MG. *Revista Árvore* 38(1): 31–40. DOI: 10.1590/S0100-67622014000100003

Fujii K., Shibata M., Kitajima K., Ichie T., Kitayama K., Turner B.L. 2018. Plant-soil interactions maintain biodiversity and functions of tropical forest ecosystems. *Ecological Research* 33(1): 149–160. DOI: 10.1007/s11284-017-1511-y

Gandolfi S., Leitão-Filho H.F., Bezerra C.L.F. 1995. Levantamento florístico e caráter sucessional das espécies arbustivo-arbóreas de uma floresta mesófila semidecídua no município de Guarulhos, SP. *Revista Brasileira de Biologia* 55(4): 753–767.

Gann G.D., McDonald T., Walder B., Aronson J., Nelson C.R., Jonson J., Hallett J.G., Eisenberg C., Guariguata M.R., Liu J., Hua F., Echeverría C., Gonzales E., Shaw N., Decleer K., Dixon K. 2019. International principles and standards for the practice of ecological restoration. Second edition. *Restoration Ecology* 27(S1): S1–S46. DOI: 10.1111/rec.13035

Garnier E., Cortez J., Billès G., Navas M.L., Roumet C., Debussche M., Laurent G., Blanchard A., Aubry D., Bellmann A., Neill C., Toussaint J.P. 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85(9): 2630–2637. DOI: 10.1890/03-0799

Gei M., Rozendaal D.M.A., Poorter L., Bongers F., Sprent J.I., Garner M.D., Aide T.M., Andrade J.L., Balvanera P., Becknell J.M., Brancalion P.H.S., Cabral G.A.L., César R.G., Chazdon R.L., Cole R.J., Colletta G.D., de Jong B., Denslow J.S., Dent D.H., DeWalt S.J., Dupuy J.M., Durán S.M., do Espírito Santo M.M., Fernandes G.W., Nunes Y.R.F., Finegan B., Moser V.G., Hall J.S., Hernández-Stefanoni J.L., Junqueira A.B. et al. 2018. Legume abundance along successional and rainfall gradients in Neotropical forests. *Nature Ecology and Evolution* 2(7): 1104–1111. DOI: 10.1038/s41559-018-0559-6

Goebel P.C., Wyse T.C., Corace R.G. 2005. Determining reference ecosystem conditions for disturbed landscapes within the context of contemporary resource management issues. *Journal of Forestry* 103(7): 351–356. DOI: 10.1093/jof/103.7.351

Higgs E., Falk D.A., Guerrini A., Hall M., Harris J., Hobbs R.J., Jackson S.T., Rhemtulla J.M., Throop W. 2014. The changing role of history in restoration ecology. *Frontiers in Ecology and the Environment* 12(9): 499–506. DOI: 10.1890/110267

Hobbs R.J., Harris J.A. 2001. Restoration ecology: repairing the earth's ecosystems in the new millennium. *Restoration Ecology* 9(2): 239–246. DOI: 10.1046/j.1526-100x.2001.009002239.x

John R., Dalling J.W., Harms K.E., Yavitt J.B., Stallard R.F., Mirabello M., Hubbell S.P., Valencia R., Navarrete H., Vallejo M., Foster R.B. 2007. Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences of the United States of America* 104(3): 864–869. DOI: 10.1073/pnas.0604666104

Kattge J., Díaz S., Lavorel S., Prentice I.C., Leadley P., Bönisch G., Garnier E., Westoby M., Reich P.B., Wright I.J., Cornelissen J.H.C., Violle C., Harrison S.P., Van Bodegom P.M., Reichstein M., Enquist B.J., Soudzilovskaia N.A., Ackerly D.D., Anand M., Atkin O., Bahn M., Baker T.R., Baldocchi D., Bekker R., Blanco C.C., Blonder B., Bond W.J., Bradstock R., Bunker D.E., Casanoves F. et al. 2011. TRY – a global database of plant traits. *Global Change Biology* 17(9): 2905–2935. DOI: 10.1111/j.1365-2486.2011.02451.x

Keenleyside K.A., Dudley N., Cairns S., Hall C.M., Stolton S. 2012. Ecological restoration for Protected Areas: Principles, guidelines and best practices. Gland, Switzerland: IUCN. 120 p.

Kindt R. 2020. WorldFlora: An R package for exact and fuzzy matching of plant names against the World Flora Online taxonomic backbone data. *Applications in Plant Sciences* 8(9): e11388. DOI: 10.1002/aps3.11388

Kollmann J., Meyer S.T., Bateman R., Conradi T., Gossner M.M., Mendonça M.S., Fernandes G.W., Hermann J.M., Koch C., Müller S.C., Oki Y., Overbeck G.E., Paterno G.B., Rosenfield M.F., Toma T.S.P., Weisser W.W. 2016. Integrating ecosystem functions into restoration ecology – recent advances and future directions. *Restoration Ecology* 24(6): 722–730. DOI: 10.1111/rec.12422

Kong F., Chen X., Zhang M., Liu Y., Jiang S., Chisholm R.A., He F. 2023. Pioneer tree species accumulate higher neighbourhood diversity than late-successional species in a subtropical forest. *Forest Ecology and Management* 531: 120740. DOI: 10.1016/j.foreco.2022.120740

Laughlin D.C. 2014. Applying trait-based models to achieve functional targets for theory-driven ecological restoration. *Ecology Letters* 17(7): 771–784. DOI: 10.1111/ele.12288

Lewis S.L., Edwards D.P., Galbraith D. 2015. Increasing human dominance of tropical forests. *Science* 349(6250): 827–832. DOI: 10.1126/science.aaa9932

Lorenzi H. 1992. *Árvores brasileiras. Manual de identificação e cultivo de plantas arbóreas nativas do Brasil*. Vol. 1. Nova Odessa, Brazil: Plantarum. 384 p.

Lorenzi H. 1998. *Árvores brasileiras: Manual de identificação e cultivo de plantas arbóreas nativas do Brasil*. Vol. 2. Nova Odessa, Brazil: Plantarum. 368 p.

Lourenço J., Newman E.A., Ventura J.A., Milanez C.R.D., Thomaz L.D., Wandekoken D.T., Enquist B.J. 2021. Soil-associated drivers of plant traits and functional composition in Atlantic Forest coastal tree communities. *Ecosphere* 12(7): e03629. DOI: 10.1002/ecs2.3629

Magalhães V.B., Espírito-Santo N.B., Salles L.F.P., Soares H., Oliveira P.S. 2018. Secondary seed dispersal by ants in Neotropical cerrado savanna: species-specific effects on seeds and seedlings of *Siparuna guianensis* (Siparunaceae). *Ecological Entomology* 43(5): 665–674. DOI: 10.1111/een.12640

Magnago L.F.S., Magrach A., Laurance W.F., Martins S.V., Meira-Neto J.A.A., Simonelli M., Edwards D.P. 2015. Would protecting tropical forest fragments provide carbon and biodiversity cobenefits under REDD+?. *Global Change Biology* 21(9): 3455–3468. DOI: 10.1111/gcb.12937

Marques M.C.M., Grelle C.E.V. (Eds.). 2021. *The Atlantic Forest: History, biodiversity, threats and opportunities of the mega-diverse forest*. Switzerland: Springer Nature. 517 p. DOI: 10.1007/978-3-030-55322-7

Menino G.C.O., Nunes Y.R.F., Tolentino G.S., Santos R.M., Azevedo I.F.P., Veloso M.D.M., Fernandes G.W. 2009. A regeneração natural da vegetação ciliar do rio Pandeiros como indicativo da futura composição da comunidade arbórea. *MG Biota* 2: 36–51.

Menino G.C.O., Nunes Y.R.F., Santos R.M., Fernandes G.W., Fernandes L.A. 2012. Environmental heterogeneity and natural regeneration in riparian vegetation of the Brazilian semi-arid region. *Edinburgh Journal of Botany* 69(1): 29–51. DOI: 10.1017/S0960428611000400

Metzger J.P., Bustamante M.M.C., Ferreira J., Fernandes G.W., Librán-Embid F., Pillar V.D., Prist P.R., Rodrigues R.R., Veira I.C.G., Overbeck G.E. 2019. Why Brazil needs its legal reserves. *Perspectives in Ecology and Conservation* 17(3): 91–103. DOI: 10.1016/j.pecon.2019.07.002

Miller J.R., Hobbs R.J. 2007. Habitat Restoration – Do We Know What We're Doing?. *Restoration Ecology* 15(3): 382–390. DOI: 10.1111/j.1526-100X.2007.00234.x

Miller S.J., Pruitt B.A., Theiling C.H., Fischer J.C., Komlos S. 2012. *Reference concepts in ecosystem restoration and environmental benefits analysis (EBA): Principles and practices.* Vicksburg, USA: Army Corps of Engineers Vicksburg Ms Engineer Research and Development Center. 18 p.

Miranda C.C., Donato A., Figueiredo P.H.A., Bernini T.A., Roppa C., Trece I.B., Barros L.O. 2019. Levantamento fitossociológico como ferramenta para a restauração florestal da Mata Atlântica, no Médio Paraíba do Sul. *Ciência Florestal* 29(4): 1601–1613. DOI: 10.5902/1980509833042

Mueller-Dombois D., Ellenberg H. 1974. *Aims and methods of vegetation ecology*. New York, USA: Wiley. 547 p.

Murray-Smith C., Brummitt N.A., Oliveira-Filho A.T., Bachman S., Moat J., Lughadha E.M., Lucas E.J. 2009. Plant diversity hotspots in the Atlantic Coastal Forests of Brazil. *Conservation Biology* 23(1): 151–163. DOI: 10.1111/j.1523-1739.2008.01075.x

Negrini M., Aguiar M.D., Vieira C.T., Silva A.C., Higuchi P. 2012. Dispersão, distribuição espacial e estratificação vertical da comunidade arbórea em um fragmento florestal no Planalto Catarinense. *Revista Árvore* 36(5): 919–930. DOI: 10.1590/S0100-67622012000500014

Nestler J.M., Theiling C.H., Lubinski K.S., Smith D.L. 2010. Reference condition approach to restoration planning. *River Research and Applications* 26(10): 1199–1219. DOI: 10.1002/rra.1330

Oliveira L.S.B., Marangon L.C., Feliciano A.L.P., de Lima A.S., Cardoso M.O., da Silva V.F. 2011. Florística, classificação sucessional e síndromes de dispersão em um remanescente de Floresta Atlântica, Moreno-PE. *Revista Brasileira de Ciências Agrárias* 6(3): 502–507. DOI: 10.5039/agraria.v6i3a1384

Oliveira P.E.A.M., Paula F.R. 2001. Fenologia e biologia reprodutiva de plantas de matas de galeria. In: J.F. Ribeiro, C.E.L. Fonseca, J.C. Sousa-Silva (Eds.): *Cerrado: caracterização e recuperação de Matas de Galeria*. Planaltina, Brazil: EMBRAPA Cerrados. P. 303–328.

Pavoine S. 2020. Adiv: An R package to analyse biodiversity in ecology. *Methods in Ecology and Evolution* 11(9): 1106–1112. DOI: 10.1111/2041-210X.13430

Pavoine S., Vela E., Gachet S., Bélair G., Bonsall M.B. 2011. Linking patterns in phylogeny, traits, abiotic variables and space: a novel approach to linking environmental filtering and plant community assembly. *Journal of Ecology* 99(1): 165–175. DOI: 10.1111/j.1365-2745.2010.01743.x

Quinn G.P., Keough M.J. 2002. *Experimental design and data analysis for biologists*. Cambridge, UK: Cambridge University Press. 537 p. DOI: 10.1017/CBO9780511806384

R Core Team. 2018. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available from https://www.r-project.org/

Ribeiro M.C., Martensen A.C., Metzger J.P., Tabarelli M., Scarano F., Fortin M.J. 2011a. The Brazilian Atlantic Forest: a shrinking biodiversity hotspot. In: F.E. Zachos, J.C. Habel (Eds.): *Biodiversity hotspots: distribution and protection of conservation priority areas*. Berlin, Germany: Springer. P. 405–434. DOI: 10.1007/978-3-642-20992-5_21

Ribeiro R.A., Lemos-Filho J.P., Ramos A.C.S., Lovato B.M. 2011b. Phylogeography of the endangered rosewood *Dalbergia nigra* (Fabaceae): insights into the evolutionary history and conservation of the Brazilian Atlantic Forest. *Heredity* 106(1): 46–57. DOI: 10.1038/hdy.2010.64

Ricotta C., Pavoine S., Bacaro G., Acosta A.T.R. 2012. Functional rarefaction for species abundance data. *Methods in Ecology and Evolution* 3(3): 519–525. DOI: 10.1111/j.2041-210X.2011.00178.x

Rigueira D.M.G., Rocha P.L.B., Mariano-Neto E. 2013. Forest cover, extinction thresholds and time lags in woody plants (Myrtaceae) in the Brazilian Atlantic Forest: resources for conservation. *Biodiversity and Conservation* 22(13–14): 3141–3163. DOI: 10.1007/s10531-013-0575-4

Rodrigues A.C., Villa P.M., Ali A., Ferreira-Júnior W., Neri A.V. 2020. Fine-scale habitat differentiation shapes the composition, structure and aboveground biomass but not species richness of a tropical Atlantic forest. *Journal of Forestry Research* 31(5): 1599–1611. DOI: 10.1007/s11676-019-00994-x

Rodrigues P.M.S., Silva J.O., Schaefer C.E.G.R. 2019. Edaphic properties as key drivers for woody species distributions in tropical savannic and forest habitats. *Australian Journal of Botany* 67(1): 70–80. DOI: 10.1071/BT17241

Rosenfield M.F., Müller S.C. 2017. Predicting restored communities based on reference ecosystems using a trait-based approach. *Forest Ecology and Management* 391: 176–183. DOI: 10.1016/j.foreco.2017.02.024

Sánchez L.E., Alger K., Alonso L., Barbosa F., Brito M.C., Laureano F., May P., Roeser H., Kakabadse Y. 2018. *Impacts of the Fundão dam failure. A pathway to sustainable and resilient mitigation*. Rio Doce Panel Thematic Repot №1. Gland, Switzerland: IUCN. 38 p.

Sansevero J.B.B., Prieto P.V., de Moraes L.F.D., Rodrigues P.J.F.P. 2011. Natural regeneration in plantations of native trees in lowland Brazilian Atlantic Forest: community structure, diversity, and dispersal syndromes. *Restoration Ecology* 19(3): 379–389. DOI: 10.1111/j.1526-100X.2009.00556.x

SER. 2004. *The SER international primer on ecological restoration*. Tucson, USA: Society for Ecological Restoration International Science & Policy Working Group. Available from https://www.ser.org/resource/resmgr/custompages/publications/SER_Primer/ser_primer.pdf

Silva F.C., Eira P.A., van Raij B., Silva C.A., Abreu C.A., Gianello C., Pérez D.V., Quaggio J.A., Tedesco M.J., Abreu M.F., Barreto W.O. 1999. Análises químicas para a avaliação da fertilidade do solo. In: F.C. Silva (Ed.): *Manual de análises químicas de solos, plantas e fertilizantes*. Brasília, Brazil: Embrapa. P. 75–169.

Silva Júnior A.L., Cabral R.L.R., Sartori L., Souza L.C., Miranda F.D., Caldeira M.V.W., Moreira S.O., Godinho T.O. 2020. Evaluation of diversity and genetic structure as strategies for conservation of natural populations of *Dalbergia nigra* (Vell.) Allemão ex Benth. *Cerne* 26(4): 435–443. DOI: 10.1590/01047760202026042754

Silva Júnior A.L., Cabral R.L.R., Sartori L., Miranda F.D., Caldeira M.V.W., Moreira S.O., Godinho T.O., Oliveira F.S. 2022. Molecular markers applied to the genetic characterization of *Dalbergia nigra*: implications for conservation and management. *Trees* 36(5): 1539–1557. DOI: 10.1007/s00468-022-02309-w

Suding K., Higgs E., Palmer M., Callicott J.B., Anderson C.B., Baker M., Gutrich J.J., Hondula K.L., LaFevor M.C., Larson B.M., Randall A., Ruhl J.B., Schwartz K.Z. 2015. Committing to ecological restoration. *Science* 348(6235): 638–640. DOI: 10.1126/science.aaa4216

Suganuma M.S., Assis G.B., Melo A.C.G., Durigan G. 2013. Ecossistemas de referência para restauração de matas ciliares: existem padrões de biodiversidade, estrutura florestal e atributos funcionais?. *Revista Árvore* 37(5): 835–847. DOI: 10.1590/S0100-67622013000500006

Tabarelli M., Villani J.P., Mantovani W. 1994. Estudo comparativo da vegetação de dois trechos de floresta secundária no núcleo Santa Virgínia, Parque Estadual da Serra do Mar, SP. *Revista do Instituto Florestal* 6: 1–11. DOI: 10.24278/2178-5031.19946499

Temperton V.M., Buchmann N., Buisson E., Durigan G., Kazmierczak Ł., Perring M.P., Dechoum M.S., Veldman J.W., Overbeck G.E. 2019. Step back from the forest and step up to the Bonn Challenge: how a broad ecological perspective can promote successful landscape restoration. *Restoration Ecology* 27(4): 705–719. DOI: 10.1111/rec.12989

Toma T.S.P., Overbeck G.E., Mendonça M.S., Fernandes G.W. 2023. Optimal references for ecological restoration: the need to protect references in the tropics. *Perspectives in Ecology and Conservation* 21(1): 25–32. DOI: 10.1016/j.pecon.2023.01.003

Turchetto F., Araujo M.M., Callegaro R.M., Griebeler A.M., Mezzomo J.C., Berghetti Á.L.P., Rorato D.G. 2017. Phytosociology as a tool for forest restoration: a study case in the extreme South of Atlantic Forest Biome. *Biodiversity and Conservation* 26(6): 1463–1480. DOI: 10.1007/s10531-017-1310-3

van der Sande M.T., Powers J.S., Kuyper T.W., Norden N., Salgado-Negret B., Almeida J.S., Bongers F., Delgado D., Dent D.H., Derroire G., do Espirito Santo M.M., Dupuy J.M., Fernandes G.W., Finegan B., Gavito M.E., Hernández-Stefanoni J.L., Jakovac C.C., Jones I.L., Veloso M.D.M., Meave J.A., Mora F., Muñoz R., Pérez-Cárdenas N., Piotto D., Álvarez-Dávila E., Caceres-Siani Y., Dalban-Pilon C., Dourdain A., Du D.V., Villalobos D.G. et al. 2023. Soil resistance and recovery during neotropical forest succession. *Philosophical Transactions of the Royal Society B: Biological Sciences* 378(1867): 20210074. DOI: 10.1098/rstb.2021.0074

Varty N. 1998. *Dalbergia nigra* (errata version published in 2016). In: *The IUCN Red List of Threatened Species 1998: e.T32985A86221269*. Available from https://dx.doi.org/10.2305/IUCN.UK.1998.RLTS.T32985A9741135.en

Veloso M.D.M., Nunes Y.R.F., Azevedo I.F.P., Rodrigues P.M.S., Fernandes L.A., Santos R.M.D., Fernandes G.W., Pereira J.A.A. 2014. Floristic and structural variations of the arboreal community in relation to soil properties in the Pandeiros river riparian forest, Minas Gerais, Brazil. *Interciencia* 39(9): 628–636.

Whitham T.G., Bailey J.K., Schweitzer J.A., Shuster S.M., Bangert R.K., LeRoy C.J., Lonsdorf E.V., Allan G.J., DiFazio S.P., Potts B.M., Fischer D.G., Gehring C.A., Lindroth R.L., Marks J.C., Hart S.C., Wimp G.M., Wooley S.C. 2006. A framework for community and ecosystem genetics: from genes to ecosystems. *Nature Reviews Genetics* 7(7): 510–523. DOI: 10.1038/nrg1877

ЭТАЛОННЫЕ УЧАСТКИ ПРИБРЕЖНЫХ АТЛАНТИЧЕСКИХ ЛЕСОВ, НАХОДЯЩИЕСЯ ПОД УГРОЗОЙ ИСЧЕЗНОВЕНИЯ В ВЕРХНЕЙ ЧАСТИ ВОДОРАЗДЕЛА РИУ-ДОСИ

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Наиболее важной особенностью экологического восстановления является выявление эталонных экосистем, которые могут служить для сравнения биологической целостности, структуры и функций экосистем. Чтобы проекты по восстановлению и сохранению экосистем были эффективными в современном сценарии снижения биоразнообразия и экосистемных услуг во всем мире, крайне важно понимать взаимодействие почвы и растений в каждой среде обитания. В этом исследовании мы оценили структуру и состав флоры на 45 участках, равномерно распределенных на трех охраняемых территориях (эталонных экосистемах) Атлантического леса в верхней части водораздела Риу-Доси на юго-востоке Бразилии. Мы также проверили, влияют ли на различия в видовом составе эдафические факторы в ярусе деревьев и ярусе подроста. В обоих ярусах наибольшим числом видов были представлены семейства Fabaceae, Myrtaceae и Lauraceae. Также для семейства Fabaceae было отмечено наивысшее значение значимости в обоих ярусах. Почвы прибрежных лесов на исследованных участках отличались высокой неоднородностью. Анализ коинерции показал явный эдафически-флористический градиент как для яруса деревьев (RV = 0.467; $p < 0.001$), так и для яруса подроста (RV = 0.478; $p < 0.001$) со связью 46.7% и 47.8% между эдафической и флористической матрицами для деревьев и подроста соответственно. На каждом исследуемом участке мы определили группы видов деревьев и подроста, которые были тесно связаны с почвами либо более богатыми, либо более бедными питательными веществами. Понимание того, как особенности экологии и жизненного цикла растений связаны с эдафическими факторами, является важным шагом на пути получения научно обоснованных знаний для поддержки политики восстановления экосистем на участках водораздела Риу-Доси.

Ключевые слова: взаимоотношения таксон – окружающая среда, охраняемый лес, структура растительности, фитоценология, ярус деревьев, ярус подроста

LONG-TERM CHANGES IN POPULATION SIZE AND DISTRIBUTION OF *STERCORARIUS MACCORMICKI* (STERCORARIIDAE, CHARADRIIFORMES) ON THE HASWELL ISLANDS, EAST ANTARCTICA

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Long-term studies are crucial in ecology, environmental change assessment, resource management and biodiversity conservation. *Stercorarius maccormicki* (hereinafter – south polar skua) are predators that can threaten populations of bird species of the orders Sphenisciformes and Procellariiformes. At many places in Antarctica, abundance trends for the skua are not known or have not been updated. This study is an attempt to answer the question: how did a south polar skua population react to changes in environmental conditions during 1956–2013? The objectives of the study was (1) to establish the dynamics of the breeding skua population on the Haswell Islands, i.e. Haswell Island and the small islands of the Haswell Archipelago during 1956–2013, and (2) to explain the reasons of the changes in the studied population. A secondary research question was whether there were changes in the spatial distribution of the breeding skua population on the Haswell Archipelago during the study period? The studies have been carried out on the Haswell Archipelago (Davis Sea), mainly in Antarctic Specially Protected Area №127 «Haswell Island and adjacent emperor penguin rookery on fast ice». Ground count was the main method for determining the size of bird colonies. South polar skua bred on 3–8 islands of the Haswell Archipelago. In the study period, the population size of the south polar skua has changed on the Haswell Archipelago. A decrease in the number of individuals (-52%) was observed between 1956–1957 and 1966–1967 breeding seasons. Between 1966–1967 and 1999–2000 breeding seasons, the skua population declined by 30.7% and reached the lowest value of 18 pairs. Population growth (344.4%) was recorded between 1999–2000 and 2009–2010 breeding seasons, with an increase of 33.8% and reaching the maximum value (83 pairs) in 2010–2011 breeding season. By 2012–2013 breeding season, the south polar skua population has declined by 13.2%. On Haswell Island, between 1956–1957 and 2012–2013 breeding seasons, there was a change in skua abundance that was similar to the change in the total breeding population on Haswell Archipelago during the entire period. On the small islands of the Haswell Archipelago, the number of breeding south polar skuas declined (-80%) between 1956–1957 and 1962–1963 breeding seasons. The breeding seasons of 1962–1963, 1966–1967 and 1999–2000 were characterised by the lowest number of individuals. Between 1999–2000 and 2009–2010 breeding seasons, the number of south polar skuas increased by 400%. A decrease in abundance (-41.6%) occurred between 2009–2010 and 2010–2011, followed by the consequent increase (by 36.3%) by 2012–2013 breeding season. During the study period, changes in the abundance of south polar skuas on the Haswell Archipelago were independent of changes in average daily November temperatures between 1956–1957 and 2012–2013 breeding seasons (Mann-Whitney test U = 0, p = 0.0017, n = 7 (asymptotic (2-sided))), when they were laying eggs and heating them. The number of south polar skuas changed independently of changes in the number of individuals of their prey, represented by *Aptenodytes forsteri*, *Pygoscelis adeliae*, and *Fulmarus glacialoides* (respectively U = 49, p = 0.0006, n = 7; U = 16, p = 0.029, n = 4; U = 16, p = 0.029, n = 4 (asymptotic (2-sided))). The high mortality of eggs, chicks and local weather conditions could influence the breeding success of the south polar skua, which could have a delayed effect on their long-term dynamics. Human activities have influenced the skua population, but have not been studied quantitatively. On the Haswell Archipelago, the reasons for historical changes in abundance of the breeding skua population remain largely unclear.

Key words: abundance, conservation, human activity, monitoring, south polar skua, tendency, trend

Introduction

Long-term studies are crucial in ecology, environmental change assessment, natural resource management and biodiversity conservation (Lindenmayer et al., 2012). They enable the tracking of changes in natural systems before and after natural and anthropogenic disturbances (Taig-Johnston et al., 2017; Philippe-Lesaffre et al., 2023). Long-term data on changes in the abundance of bird populations are valuable for identifying possible causes of fluctuations and for conservation measures (Reif, 2013). Gaps in long-term population studies contribute to less reliable explanations of the processes occurring in populations and ecosystems, as well as the causes that induce these changes. Seabirds are found in all oceans, from coastal areas to the high seas, and, compared with most other marine animals, they provide a better understanding of threats to their populations and population trends (Dias et al., 2019).

Stercorarius maccormicki (Saunders, 1893) (hereinafter – south polar skua or skua; see Fig. 1) is an opportunistic predator that breeds around Antarctica (Ritz et al., 2008), mainly on the coasts (Higgins & Davies, 1996; Carneiro et al., 2016). It is listed under the Least Concern category in the Global IUCN Red List (BirdLife International, 2018). The state of the world population of this species (6000–15 000 adults) has been assessed as stable (BirdLife International, 2018). Approximately 50% of the global skua population is estimated to inhabit the Ross Sea region (Wilson et al., 2017).

In continental Antarctica, the south polar skua is a food generalist, which uses a wide range of prey including marine mammals, penguins, flying birds, fish and invertebrates, as well as kitchen refuse and garbage (Reinhardt et al., 2000). Skuas are sensitive to human activities (Chwedorzewska & Korczak, 2010) and by breeding near stations or sites of intense human activity, they are able to benefit from this by increasing predation on eggs and chicks of other bird species (Sander et al., 2005). In East Antarctica, the south polar skua is the only avian predator that seriously affects breeding populations of seabirds (Norman & Ward, 1990), which form the basis of its diet (Reinhardt et al., 2000). Any increase in the skua population is an additional pressure on their prey, i.e. birds that may already be influenced by human activities (Hemmings, 1990).

Population trends of the skua are poorly understood (Wilson et al., 2015), and the number of skua individuals has been infrequently assessed in most locations (Wilson et al., 2017). Information on trends of the south polar skua is available on a very few sites, particularly in the last 10–20 years (Phillips et al., 2019). This is partly true because changes in skua colonies due to human activity make them less useful for monitoring of marine ecosystems than penguins, but may be useful, if such links are not present (Ainley et al., 1986). However, the skua population trends with various time ranges (i.e. an interval between the first and last population counts in a particular location) and detailing (i.e. the number of population counts in a known time range) remain the focus of interest of researchers. They are analysed and used in the monitoring of the Antarctic environment, in particular in the environmental policy of Antarctic stations and their neighbourhood (e.g. Chwedorzewska & Korczak, 2010). Research in the Antarctic Peninsula with adjacent islands (West Antarctica), Pointe Géologie, Terre Adélie (East Antarctica) and the Ross Sea region claim leadership in this direction (e.g. Ainley et al., 1986; Quintana et al., 2000; Micol & Jouventin, 2001; Grilli, 2014; Krietsch et al., 2016). However, there are still many places in Antarctica and adjacent islands where skua population trends are not known or have not been updated.

Fig. 1. South polar skua (*Stercorarius maccormicki*) on the Haswell Archipelago, Davis Sea.

The south polar skua is a common avian species, a seasonal resident of the Haswell Archipelago (East Antarctica). It breeds in loose colonies, small groups or single pairs on islands free of snow and ice. The breeding population of the skua is the least abundant compared to the size of breeding populations of other bird species, it is relatively well studied and has a long series of intermittent observations (Mawson, 1915; Korotkevich, 1959; Pryor, 1964, 1968; Syroechkovsky, 1966; Kamenev, 1968; Starck, 1980; Mizin, 2015; Golubev, 2018). The local skua population represents about 1–2% of the global adult population, where Haswell Island supports 70.0–91.5% of breeding skuas on the Haswell Archipelago.

On the Haswell Islands, the south polar skua usually feeds on eggs, chicks and adults of the most abundant bird species, such as *Aptenodytes forsteri* Gray, 1844, *Pygoscelis adeliae* (Hombron & Jacquinot, 1841), and *Fulmarus glacialoides* (Smith, 1840) (Pryor, 1968). They mainly feed on carrion (Korotkevich, 1958, 1959; Pryor, 1965; Kamenev, 1977, 1978) and rarely turn to predation (Pryor, 1968). *Pygoscelis adeliae* suffers the most from predation by skuas (Mawson, 1915; Pryor, 1964; Kamenev, 1971). At the Mirny Station, skuas also visited the food waste dump for several decades (Starck, 1980; Mizin, 2015; Golubev, 2018). South polar skuas have no food competitors on land, except for *Stercorarius antarctica lonnbergi* (Mathews, 1912), which has recently entered the Haswell Islands (Mizin, 2015; Golubev, 2020, 2021). As an avian predator, south polar skua can pose threats to other Haswell Archipelago seabird populations. Therefore, studying of the exploitation of prey trophic relationships of skuas is important for our understanding of the long-term survival and coexistence of local seabird populations. Skua interactions with their prey should be considered in Antarctic Specially Protected Area №127 «Haswell Island and adjacent emperor penguin rookery on fast ice» (hereinafter – ASPA №127 «Haswell Island»), as *Aptenodytes forsteri* and *Pygoscelis adeliae* are vulnerable and require conservation measures (BirdLife International, 2024). *Aptenodytes forsteri* is a Near Threatened taxon (BirdLife International, 2020).

Updated information on skua population trends on the Haswell Archipelago has not been published until recently (Carneiro et al., 2016). This study attempts to answer the question: how did the south polar skua population reacts to changes in environmental conditions during the period of 1956–2013? The objectives of the study were (1) to establish the dynamics of the breeding population of the skua on the Haswell Islands, i.e. Haswell Island and the small islands on the Haswell Archipelago during the period of 1956–2013, and (2) to explain the reasons for skua population changes. A secondary research interest was to answer the following question: have there been changes in the spatial distribution of the breeding skua population on the islands of the Haswell Archipelago during the study period, and if so, what has changed?

Material and Methods

Study area

Haswell Archipelago (66.55° S, 93.01° E) is located in the coastal part of the continental shelf of Davis Sea (Treshnikov Bay, Queen Mary Land, southern Indian Ocean). The area is rich in icebergs. For most of the year, the sea is covered with fast ice. Its width can exceed 30 km (Shesterikov, 1959; Mirny Observatory, 2020). The Haswell Archipelago includes 17 relatively large islands scattered no further than 3 km (excluding Ploskiy Island) from the coast of Antarctica, where the Russian Mirny Antarctic Research Station has operated year-round since 1956, providing the basis for research activities. Haswell Island is the largest (0.82 km^2) and highest (93.1 m a.s.l.) rock of the Haswell Archipelago (Voronov & Klimov, 1960; Kashin & Chistyakov, 2022; Fig. 2).

The altitude of smaller islands generally ranges from 10 m a.s.l. to 35 m a.s.l. (Voronov & Klimov, 1960). The study area (about 12 km^2) included islands and sea ice hosting breeding populations of nine bird species, namely *Aptenodytes forsteri*, *Pygoscelis adeliae*, *Oceanites oceanicus* (Kuhl, 1820), *Fulmarus glacialoides*, *Thalassoica antarctica* (J.F. Gmelin, 1789), *Daption capense* (Linnaeus, 1758), *Pagodroma nivea* (G. Forster, 1777), *Stercorarius maccormicki*, and *S. antarctica*. All bird species breeding in this area are concentrated on Haswell Island and near it (Golubev, 2018). In order to preserve this biodiversity, Site of Special Scientific Interest №7 «Haswell Island» (Report, 1976) was allocated in 1975 on the Haswell Archipelago. This Protected Area was later named as (hereinafter – ASPA №127 «Haswell Island»). Its boundaries coincide with those of Important Bird Area «ANT 141: Haswell Island» (Harris et al., 2015).

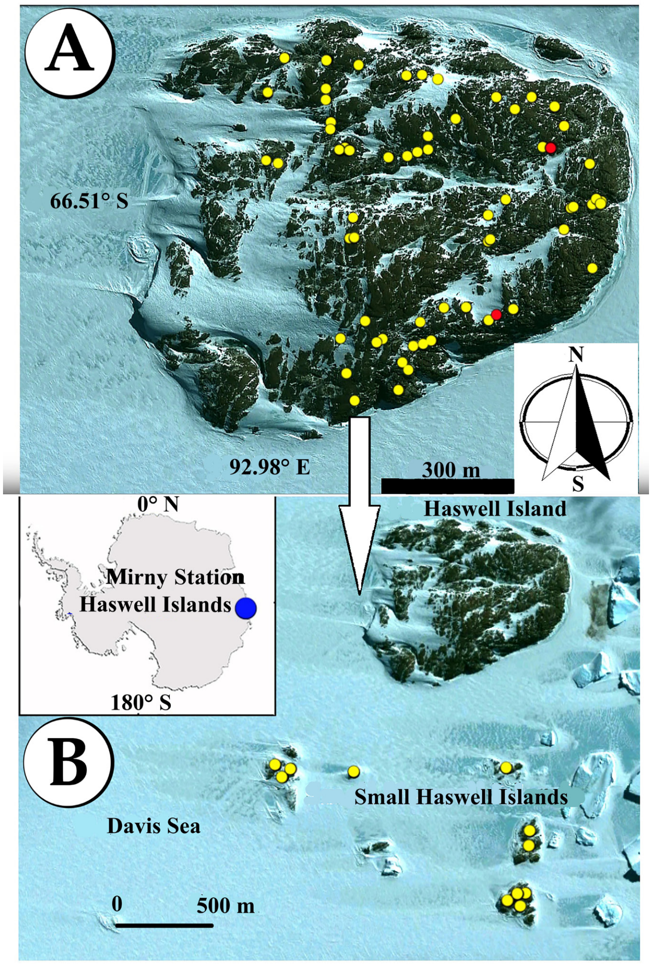

Fig. 2. Distribution of active nest sites of the skua (*Stercorarius maccormicki*) on the Haswell Islands based on 2012–2013 breeding season censuses (Fig. 2A). Yellow circles – nests of *Stercorarius maccormicki*; red circles – nests of mixed pairs (*Stercorarius maccormicki* with *S. antarctica lonnbergi* or possibly hybrid individuals between these species). The inset in the upper left corner of Fig. 2B shows the location of the study area and the Mirny Station.

Bird survey methods

The fieldwork of Sergey V. Golubev has been carried out during the 2012–2013 and 2015–2016 breeding seasons inside the Haswell Archipelago. South polar skuas were counted in November and December 2012. The counts of mixed pairs (*Stercorarius maccormicki* with *S. antarctica lonnbergi* or possibly hybrid individuals between these species) were carried out in November – January from 2012–2013 to 2015–2016. Data from 1912–1913 to 2010–2011 were taken from publications and unpublished reports of biologists (Table 1).

The research mainly covered the period of laying eggs, incubation of eggs and the beginning of chick hatching. Ground counts have been the main method for studying breeding populations of seabirds. For skuas, we counted 1) pairs with nests containing eggs or chicks, 2) adult birds sitting on nests, without clutches of eggs and chicks, 3) territorial pairs without nests. In 2012, skua surveys were carried out in November and December. During a later count (December) of the same breeding season, the status of pairs (i.e. breeding pairs or territorial pairs without nests) of adult birds sitting on nests, without clutches of eggs and chicks and territorial pairs without nests may have changed. Data analysis was based on counting breeding pairs on occupied nests. A pair with a clutch of eggs or chick(s) has been considered a breeding pair. The standard approach for counting skuas by recording territorial pairs or brooding birds in occupied territories (Carneiro et al., 2016; Krietsch et al., 2016; Phillips et al., 2019) has been used partly based on the specifics of historical information and our own data sets.

The size of skua colonies, trends of their prey (*Aptenodytes forsteri*, *Pygoscelis adeliae*, *Fulmarus glacialoides*) in the breeding skua populations on the Haswell Archipelago, and changes in the spatial distribution, abundance and population density of birds (pair/km^2) were also the focus of our attention. They were established by comparing historical (Korotkevich, 1959; Pryor, 1968; Kamenev, 1968; Starck, 1980; Mizin & Chernov, 2000; Dorofeev, 2011; Mizin, 2015) and our (from 2012–2013 to 2015–2016 breeding seasons) data. The population density of breeding skua pairs on Haswell Island was calculated together with glaciers on its surface. The geographic co-ordinates of the nest position, occupied territories, the distance from the nest to the nearest border of Haswell Island and the distance between the nearest nests with clutches of eggs without taking into account uneven terrain, as well as the height of the nests above sea level, were recorded using a GPS (Global Positioning System) navigator. Each nest with eggs or chicks was mapped using Google Earth Pro programme to eliminate double fixation (Phillips et al., 2019; Fig. 2A). Nests were photographed with one or both partners of a pair. Whenever possible, the number and combinations of coloured plastic marks, number of metal rings on legs of breeding skuas were recorded. This also contributed to the elimination of double fixation of one nest. For each nest on Haswell Island, we calculated (1) the nearest-neighbour index (NNI index) as an average distance from the nest to three other closest nests (Carneiro et al., 2010), (2) distance from the nest to the edge of the island (Carneiro et al., 2010), and (3) nest position above sea level. The number of eggs in the clutch or their absence and the standard morphometric parameters of the nest and eggs were recorded. Identification of *Stercorarius maccormicki* and *S. antarctica lonnbergi* has been carried out based on a set of features, namely size, plumage colour, voice, and posture during the demonstration of a long call. The hybrid status of transitional individuals has not been established.

Mapping of historical records of occupied south polar skua nests on Haswell Island collected by a unified way from censuses conducted from 1956–1957 to 2009–2010 breeding seasons (n = 5, Fig. 3) was based on relevantly published maps (Korotkevich, 1959; Pryor, 1968; Starck, 1980; Mizin & Chernov, 2000; Mizin, 2015). However, the distribution of nests was still approximately due to the lack of accurate co-ordinates in publications and reports or detailed maps with the location of nests in the study area.

All the islands, except for Haswell Island, were considered small islands. Statistical analysis and data visualisation were carried out in Microsoft Excel 2013 (USA), in Google Earth Pro 2022 (USA), and Adobe Photoshop CC 2015.0.0 Portable Version (USA). Calculation of statistical indicators (Mann-Whitney U-test) was carried out using the SciPy library ver. 1.11.4. (https://scipy.org/) in Python ver. 3.11 (https://www.python.org/). Calculation of the Mann-Whitney U-test for data presented with spaces, continuity correction (1/2) was applied.

Results

Changes in the abundance of the breeding population of the south polar skua on the Haswell Archipelago (from 1956–1957 to 2012–2013)

During the study period, the breeding skua population on the Haswell Archipelago has experienced changes in breeding conditions. A decline in abundance was observed between 1956–1957 and 1966–1967 breeding seasons (-52%). Following the gap between 1966–1967 and 1999–2000 breeding seasons, the skua population size experienced a 30.7% decline and reached a historically minimal value of 18 breeding pairs. Population growth (344.4%) was recorded between 1999–2000 and 2009–2010 breeding seasons, with an increase by 33.8% and by reaching a historical maximum (83 pairs) in 2010–2011 breeding season. By the 2012–2013 breeding season, the number of breeding south polar skuas had decreased by 13.2% (Fig. 4A). The number of south polar skuas changed during the study period regardless of changes in the number of their food resources, namely *Aptenodytes forsteri*, *Pygoscelis adeliae*, and *Fulmarus glacialoides* (respectively, U = 49, p = 0.0006, n = 7; U = 16, p = 0.029, n = 4, and U = 16, p = 0.029, n = 4 (asymptotic (2-sided))).

On Haswell Island, there was a change in skua abundance from 1956–1957 to 2012–2013 breeding seasons (Fig. 4B). These changes were similar to changes in the total size of the breeding skua population on all Haswell Islands during the above mentioned period (Fig. 4A). On the small islands of the Haswell Archipelago, the number of breeding skuas declined sharply (-80%) from 1956–1957 to 1962–1963 breeding seasons. The breeding seasons of 1962–1963, 1966–1967, and 1999–2000 were characterised by the lowest or near the lowest historical minimum abundance. On the small islands of the Haswell Archipelago, the number of skuas increased by 400% between 1999–2000 and 2009–2010 breeding seasons. There was a decrease in population size (-41.6%) from 2009–2010 to 2010–2011 breeding seasons, followed by an increase (36.3%) by 2012–2013 breeding season (Fig. 4C). On the small islands of the Haswell Archipelago, the skua abundance changed independently of changes in the skua abundance on Haswell Island (U = 48.5, p = 0.002 (asymptotic (2-sided))). Moreover, during the study period, changes in the skua abundance on the Haswell Islands were independent of changes in average daily November temperature from 1956–1957 to 2012–2013 breeding seasons (Mann-Whitney test: U = 0, p = 0.0017, n = 7 (asymptotic (2-sided))), when they were laying eggs and heating them.

Dynamics of the spatial distribution of the breeding skua population on the islands of the Haswell Archipelago

In the 2012–2013 breeding season, south polar skuas occupied six islands of the Haswell Archipelago, namely Haswell Island, Tokarev Island, Gorev Island, Buromsky Island, Zykov Island, and Fulmar Island. Seventy-two breeding skua pairs were identified with nests with clutches, and three territorial pairs without nests. On Haswell Island, 61 breeding pairs (84.7% of the total number of breeding skuas on the Haswell Archipelago) were found.

Table 1. Distribution and abundance of breeding pairs of the south polar skua (*Stercorarius maccormicki*) on the Haswell Islands, 1912–2013

Breeding season	Breeding pairs on islands								∑ (breeding pairs)	References
	1	2	3	4	5	6	7	8		
1912–1913	+	–	–	–	–	–	–	–	–	Mawson, 1915
1956–1957	35	3	4	3	2	1	1	1	50	Korotkevich, 1959
1962–1963	23	1	1	0	1	0	0	0	26	Pryor, 1968
1966–1967	20	4	0	0	0	0	0	0	24	Kamenev, 1968
1978–1979	20	–	–	–	–	–	–	–	–	Starck, 1980
1999–2000	15	2	1	0	0	0	0	0	18	Mizin & Chernov, 2000
2009–2010	50	3	2	3	1	1	1	1	62	Mizin, 2015
2010–2011	76	3	1	1	1	1	0	0	83	Dorofeev, 2011
2012–2013	61	4	3	2	0	1	0	1	72	S.V. Golubev, unpublished data

Note: Designations of the islands: 1 – Haswell Island; 2 – Fulmar Island; 3 – Tokarev Island; 4 – Zykov Island; 5 – Stroiteley Island; 6 – Buromsky Island; 7 – Poryadin Island; 8 – Gorev Island; «+» – skuas bred, but counts were not carried out; «–» – counts were not carried out.

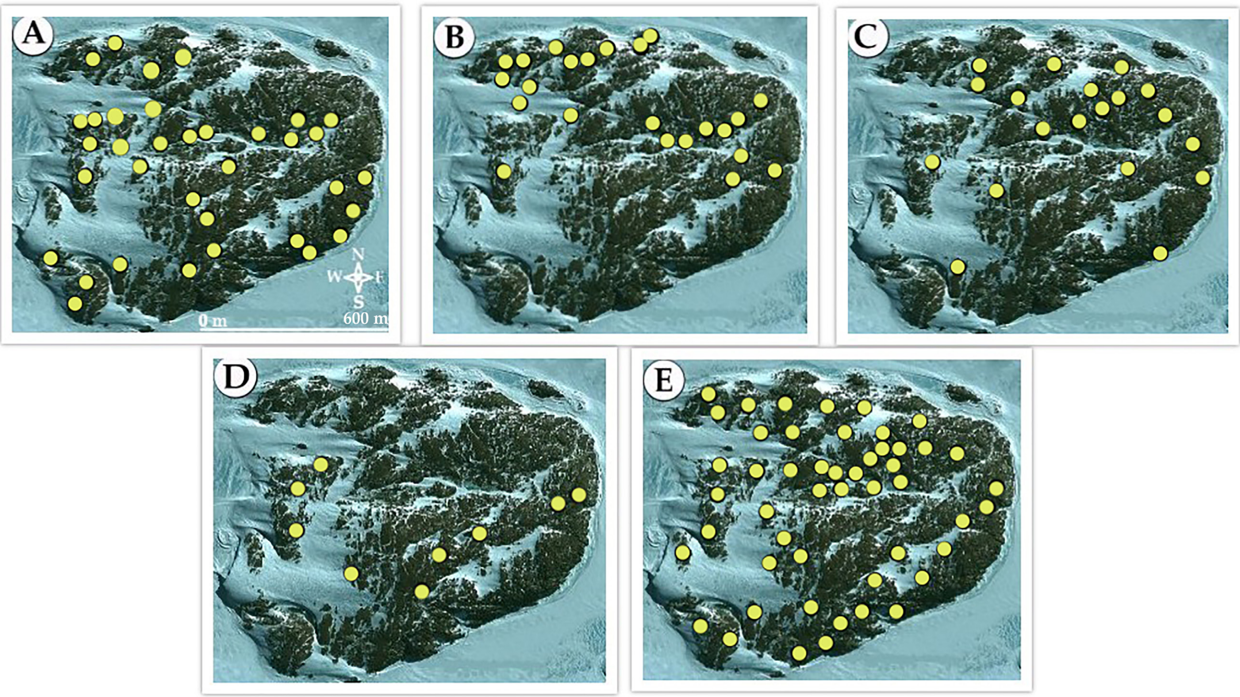

Fig. 3. Distribution of occupied nests of the south polar skua (*Stercorarius maccormicki*) on Haswell Island (yellow circles) according to surveys in a specific breeding season. Designations: A – season of 1956–1957 (redrawn from Korotkevich, 1959); B – season of 1962–1963 (redrawn from Pryor, 1968); C – season of 1978–1979 (redrawn from Starck, 1980); D – season of 1999–2000 (redrawn from Mizin & Chernov, 2000); E – season of 2009–2010 (redrawn from Mizin, 2015). Fig. 3D shows nine out of 15 nests of the south polar skua identified originally by Mizin & Chernov (2000).

Nests of mixed pairs of the skua also were identified on Haswell Island. In 2012–2013 breeding season, two nests with eggs and chicks and one territorial pair without nest were found on Haswell Island. In 2014–2015, one breeding pair was recorded on Haswell Island. In 2015–2016 breeding season, two breeding pairs and one territorial pair without nest were found on Haswell Island.

During the studied period (1912–2016), changes in the spatial distribution of south polar skua nests on the Haswell Islands have been identified. Skuas bred on 3–8 islands of the Haswell Archipelago, usually near colonies of *Pygoscelis adeliae* and species of Procellariiformes (Mawson, 1915; Korotkevich, 1959; Kamenev, 1968; Pryor, 1968; Starck, 1980; Mizin & Chernov, 2000; Dorofeev, 2011; Mizin, 2015; S.V. Golubev, unpublished data). Annual (Haswell Island and Fulmar Island) or near-annual (Tokarev Island) breeding occurred on three islands. Non-annual breeding was recorded on five islands (Zykov Island, Stroiteley Island, Buromsky Island, Poryadin Island, and Gorev Island). The rarest breeding of single pairs was observed on Poryadin Island and Gorev Island, where there were no breeding colonies of other seabird species. At breeding seasons with a relatively low bird abundance (18–26 breeding pairs), skuas occupied up to three small islands. However, they occupied up to seven small islands, if the total breeding population size was ≥ 50 pairs (Table 1).

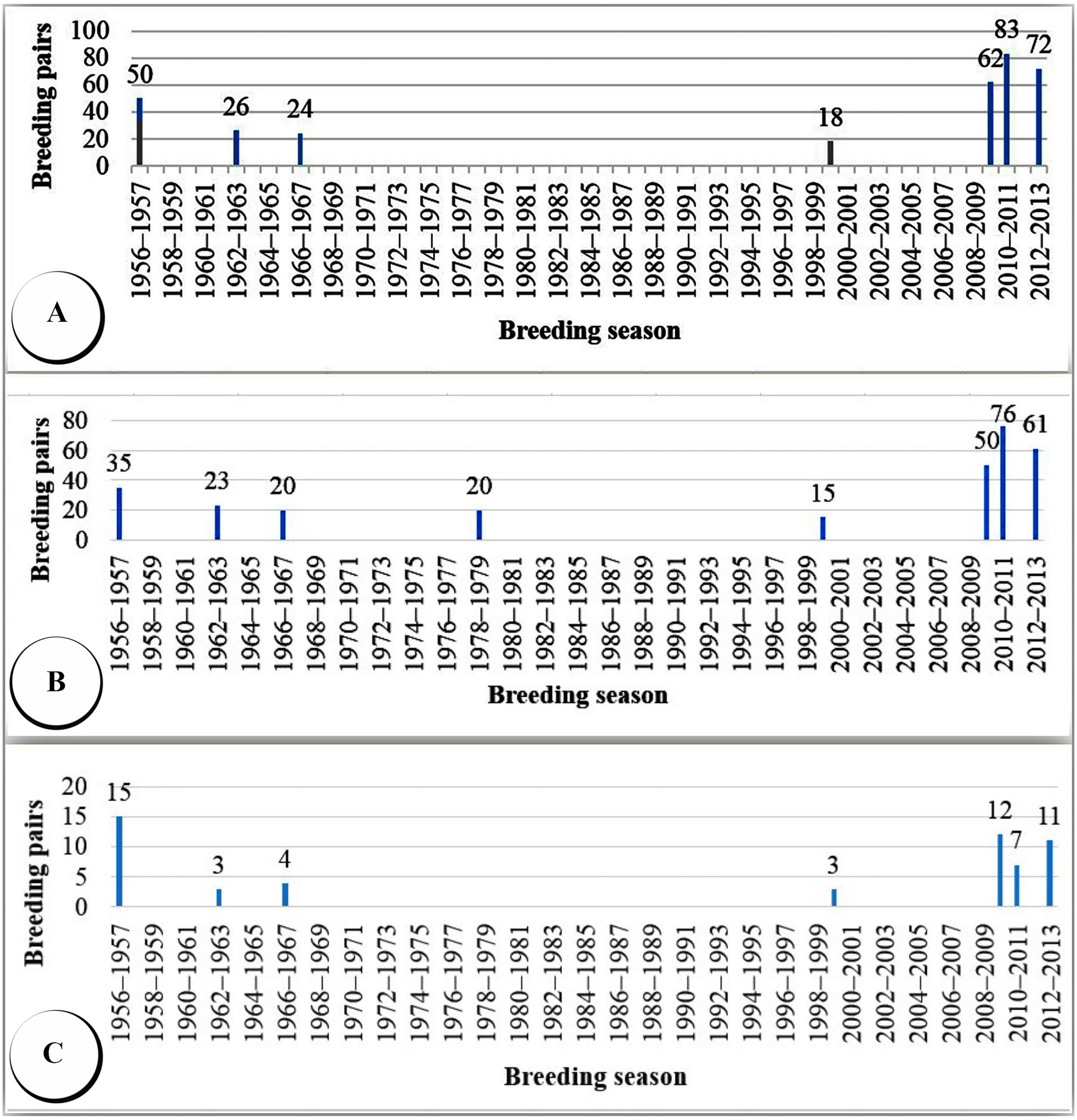

Fig. 4. Long-term changes in breeding population size of the south polar skua (*Stercorarius maccormicki*) on all islands of the Haswell Archipelago (A), on Haswell Island (B), and on the small islands of the Haswell Archipelago (C) from 1956–1957 to 2012–2013. References: Korotkevich (1959), Pryor (1968), Kamenev (1968), Starck (1980), Mizin & Chernov (2000), Dorofeev (2011), Mizin (2015), S.V. Golubev (unpublished data).

The spatial distribution of breeding skua pairs and nest density on Haswell Island varied over the study period (Fig. 2, Fig. 3). Due to the small number of breeding pairs (≤ 26 pairs), skuas tended to breed in the northern part of Haswell Island (Fig. 3B,C) or in its centre (Fig. 3D). Against this background, nest density could be either low (Fig. 3C,D) or relatively high (Fig. 2A, Fig. 3A,E). At the relatively high number (≥ 50 pairs), skuas nested from 2/3 (Fig. 2A) to the entire area of Haswell island (Fig. 3A,E). Nest placement could be relatively uniform (Fig. 3E) and locally dense (Fig. 2A, Fig. 3A). Nest density varied over the study period from 18.2 nests/km^2 to 92.6 nests/km^2, with an average of 28 nests/km^2 (n = 8). In general, the spatial distribution of active skua nests appears to be driven by environmental conditions at the beginning of a particular breeding season.

In the 2012–2013 breeding season, the distance between the nearest skua nests on Haswell Island (mean ± SE (min–max)) was 105.9 ± 9.9 m (7.0–352.2 m), with a median at 84.2 m (n = 60). The distance between mixed pairs was 413 m (n = 1). On Haswell Island, the nesting density of the south polar skua (excluding active nests of two mixed pairs) was 87.8 nests/km^2. Nests were placed on the inner surface of rocks. In the 2012–2013 breeding season, the distance from the skua nests to the nearest border of Haswell Island (mean ± SE (min–max)) was 118.0 ± 10.6 m (18–359 m) (n = 61). The distance for two nests of mixed pairs was 180 m and 78 m.

Skuas used the entire range of altitudes of Haswell Island surface to accommodate their nests. On small islands of the Haswell Archipelago, altitudes of the skua nest position (Table 2) were more than three times lower than on Haswell Island.

Compared to Haswell Island, the low location of skua nests on small islands was observed only as a result of their low altitude values. On Haswell Island, the vertical distribution of south polar skua nests follows a normal distribution (Fig. 5).

In December 2012, full clutches of the south polar skua contained one (n = 8) or two (n = 64) eggs. In nests of mixed pairs, two chicks (n = 1) and two eggs (n = 1) were found. The egg size (length × width) of the skua was 73.2 ± 2.7 mm (65.0–81.2 mm) × 51.3 ± 1.2 mm (48.0–55.1 mm) (n = 128). In the two nests of mixed pairs, the egg size was 74.1 × 52.6 mm, and 74.1 × 51.8 mm. The nest size of the south polar skua (n = 68) was 243.6 ± 19.5 mm (190–290 mm) × 261.4 ± 112.7 mm (230–340 mm). The nest size of one mixed pair (n = 1) was 280 × 290 mm.

Discussion

Skua population dynamics have been monitored on the Haswell Archipelago, a part of East Antarctica. Here warming or cooling conditions were relatively stable between 1956 and 2018, and no widespread cooling was observed at East Antarctic stations in recent decades (Turner et al., 2019). The results of the research established that the number of the south polar skuas changed regardless of changes in the number of their most abundant prey. However, early cleaning of the coastal water area from fast ice (for example, in December), where south polar skuas feed on sea ice with frozen eggs and chicks of *Aptenodytes forsteri* at the beginning of the breeding season, could negatively affect the state of the skua population. At the same time, during the seasons of decrease in number of skua individuals (namely 1962–1963, 1966–1967, 1978–1979), phenological data on the destruction of fast ice were not recorded by researchers, but were suitable in the 1999–2000 breeding season (Antipov & Molchanov, 2022). Then the size of the breeding population reached a historical minimum of 18 breeding pairs.

During long-term monitoring, the mass mortality of adult skuas on the Haswell Archipelago has not been established (Korotkevich, 1959; Pryor, 1968; Kamenev, 1968; Starck, 1980; Mizin, 2015; Golubev, 2018), as well as the mortality of young and adult birds during the marine stage of the annual cycle (migration and wintering). Mortality of adults during the breeding season is very low (usually one or two adults were recorded).

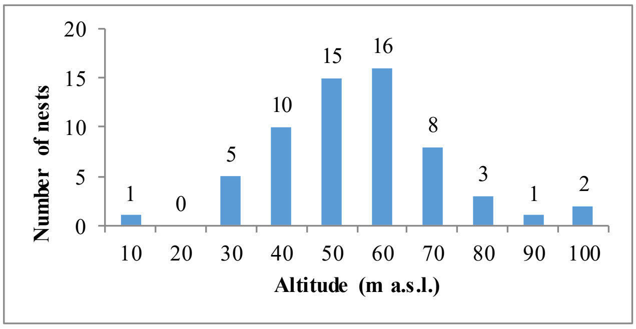

Fig. 5. Altitude distribution of south polar skua (*Stercorarius maccormicki*) nests on the Haswell Island in the 2012–2013 breeding season.

Table 2. Nesting altitude (m a.s.l.) of the south polar skua (*Stercorarius maccormicki*) and mixed pairs (*Stercorarius maccormicki* with *S. antarctica lonnbergi* or possibly hybrid individuals between these species) on the Haswell Islands at 2012–2013 breeding season

Islands	m	SE	min	max	n
Stercorarius maccormicki					
Haswell	49.9	2	6	93	61
Small islands	13.3	2.8	4	30	11
Total	44.3	2.3	4	93	72
Mixed pairs					
Haswell	48.5	0	43	54	2

Note: m – average value, SE – standard error, min – minimum value, max – maximum value, n – number of nests.

At the same time, brood (eggs and chicks) mortality was relatively high. For example, by 05.01.1963, it was 55%, of which egg losses accounted for about 68% (Pryor, 1968), and by 07.01.1967, the survival of chicks was 45% of the total number of laid eggs (Kamenev, 1968). During the study period, the reproductive success (the ratio of the number of fledged young birds capable of flying to the total number of eggs laid) of the skua has not been studied. However, sibling aggression of chicks and local weather conditions (increased winds, heavy precipitation and sharp changes in the surface temperature) of a particular breeding season could influence the breeding success of the skua, which could have a delayed effect on the long-term dynamics of their breeding population.

Partial loss and habitat modification (Pryor, 1965; Propp, 1968; Golubev, 2021), direct persecution of the skua in the Mirny Station (Propp, 1968), bird hunting, collection of eggs and chicks for scientific purposes (Yudin, 1958; Korotkevich, 1959; Makushok, 1959; Kirpichnikov, 1965; Syroechkovsky, 1966) negatively affected the skua population. Long-term use of food waste from the Mirny Station for decades (Starck, 1980; Mizin, 2015; Golubev, 2018) could positively influence the maintenance of the skua population. However, food waste is used primarily by non-breeding individuals. Thus, the human activity has influenced the breeding skua population over the study period. Nevertheless, this influence has not been quantified.

Conclusions

Our study completes the general picture of the knowledge state on long-term trends in the skua abundance in Antarctica and the reasons that may affect the annual changes in the skua abundance. Considerable gaps in the measurement of abundance, breeding success and the impact of human activities on the skua population over the study period have induced difficulties in interpreting the existing data set. In general, reasons for changes in the skua abundance on the Haswell Islands remain highly unclear. Greater clarity in understanding of the interactions between avian predators and their prey against the backdrop of a changing climate could facilitate the adoption of adequate measures to conserve the overall abundance of life on the Haswell Islands, if necessary.

Dynamic interactions of ecological variables limit the possibility of reliable identification of the causes determining trends in the number of individuals in skua populations and do not allow us making a clear distinction between the influences of certain factors. The difficulty in interpreting the results is related to the close interweaving of environmental factors, their synergistic effect, the influence of human activities, and the poor knowledge on the skua existence during the marine period of their annual cycle. Sometimes it is easier to explain the causes of changes by anthropogenic factors than by natural factors, and even more so by their combined interaction.

Progress in trend studies can be made if the results of long-term monitoring of south polar skua populations in Antarctica are considered and interpreted along with detailed studies and involving as many aspects as possible related to the life of the skua and their interactions with the environment they inhabit. It is likely that in the near future, the results of analysis of long-term monitoring of those (ideal) skua populations, which breeding sites are remote and free from human activity, but well documented for decades, will be of increasing value. Of particular scientific interest should be the breeding skua populations in the inland hard-to-reach parts of Antarctica. At such places their interactions with the environment are perhaps simpler and more straightforward than on the coast of the mainland and islands, where predator-prey interactions remain virgin, as in the prehistoric era. An undoubted continuation of monitoring and an increase in the number of publications of updated trends of local skua populations can be expected from sites with a long history where the human population density in Antarctica is relatively high.

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References

Ainley D.G., Morrell S.H., Wood R.C. 1986. South Polar skua breeding colonies in the Ross Sea region, Antarctica. *Notornis* 33: 155–163.

Antipov N.N., Molchanov M.S. (Eds.). 2022. Station Mirny. Hydrometeorological regime of the region.

Regime and reference manual (Electronic resource). St. Petersburg: AARI. 208 p. [In Russian]

BirdLife International. 2018. *Catharacta maccormicki*. In: *The IUCN Red List of Threatened Species 2018: e.T22694218A132533643*. Available from https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T22694218A132533643.en

BirdLife International. 2020. *Aptenodytes forsteri*. In: *The IUCN Red List of Threatened Species 2020: e.T22697752A157658053*. Available from https://dx.doi.org/10.2305/IUCN.UK.2020-3.RLTS.T22697752A157658053.en

BirdLife International. 2024. *IUCN Red List for birds*. Available from http://datazone.birdlife.org

Carneiro A.P.B., Polito M.J., Sander M., Trivelpiece W.Z. 2010. Abundance and spatial distribution of sympatrically breeding *Catharacta* spp. (Skuas) in Admiralty Bay, King George Island, Antarctica. *Polar Biology* 33(5): 673–682. DOI: 10.1007/s00300-009-0743-x

Carneiro A.P.B., Manica A., Phillips R.A. 2016. Long-term changes in population size, distribution and productivity of skuas (*Stercorarius* spp.) at Signy Island, South Orkney Islands. *Polar Biology* 39: 617–625. DOI: 10.1007/s00300-015-1817-6

Chwedorzewska K.J., Korczak M. 2010. Human impact upon the environment in the vicinity of Arctowski Station, King George Island, Antarctica. *Polish Polar Research* 31(1): 45–60. DOI: 10.4202/ppres.2010.04

Dias M.P., Martin R., Pearmain E.J., Burfield I.J., Small C., Phillips R.A., Yates O., Lascelles B., Borboroglu P.G., Croxall J.P. 2019. Threats to seabirds: A global assessment. *Biological Conservation* 237: 525–537. DOI: 10.1016/j.biocon.2019.06.033

Dorofeev D.S. 2011. *Report on the ecological and environmental studies at the Mirny Station during 55th RAE*. Unpublished report. 28 p. [In Russian]

Golubev S.V. 2018. Injuries of Webs on the Feet of South Polar Skuas *Catharacta Maccormicki*: Results of Studying Active Obliged Aggregations. *American Journal of Life Sciences* 6(5): 65–73. DOI: 10.11648/j.ajls.20180605.12

Golubev S. 2020. Vagrants and visitors in the avifauna of the Haswell archipelago, East Antarctica. *Polish Polar Research* 41(2): 137–150. DOI: 10.24425/ppr.2020.133010

Golubev S. 2021. Seabirds of human settlements in Antarctica: A case study of the Mirny Station. *Czech Polar Reports* 11(1): 98–113. DOI: 10.5817/CPR2021-1-8

Grilli M.G. 2014. Decline in numbers of Antarctic skuas breeding at Potter Peninsula, King George Island, Antarctica. *Marine Ornithology* 42(2): 161–162.

Harris C.M., Lorenz K., Fishpool L.D.C., Lascelles B., Cooper J., Coria N.R., Croxall J.P., Emmerson L.M., Fijn R.C., Fraser W.L., Jouventin P., LaRue M.A., Le Maho Y., Lynch H.J., Naveen R., Patterson-Fraser D.L., Peter H.U., Poncet S., Phillips R.A., Southwell C.J., van Franeker J.A., Weimerskirch H., Wienecke B., Woehler E.J. 2015. *Important Bird Areas in Antarctica 2015*. Cambridge: BirdLife International and Environmental Research & Assessment Ltd. 301 p. DOI: 10.13140/RG.2.1.1554.2884

Hemmings A.D. 1990. Human impacts and ecological constraints on skuas. In: K.R. Kerry, G. Hempel (Eds.): *Antarctic ecosytems: ecological change and conservation*. Berlin: Springer-Verlag. P. 224–230. DOI: 10.1007/978-3-642-84074-6_24

Higgins P.J., Davies S.J.J.F. (Eds.). 1996. *Handbook of Australian, New Zealand and Antarctic birds. Vol. 3: Snipe to Pigeon. Part A*. Melbourne: Oxford University Press. 1028 p.

Kamenev V.M. 1968. Ornithological observations in the Mirny area in 1966/67. *Newsletter of the Soviet Antarctic Expedition* 67: 72–74. [In Russian]

Kamenev V.M. 1971. Ecology of the Adélie penguins of the Haswell Islands. *Newsletter of the Soviet Antarctic Expedition* 82: 67–71. [In Russian]

Kamenev V.M. 1977. Ecology of emperor penguins in the area of the Haswell archipelago (East Antarctica). In: *Adaptations of penguins*. Moscow: Nauka. P. 141–156. [In Russian]

Kamenev V.M. 1978. Silver-gray petrel (*Fulmarus glacialoides*) of the Haswell archipelago. *Newsletter of the Soviet Antarctic Expedition* 98: 76–82. [In Russian]

Kashin S.V., Chistyakov I.A. 2022. Physical and geographical description of the area of the Station Mirny. In: N.N. Antipov, M.S. Molchanov (Eds.): *Station Mirny. Hydrometeorological regime of the region*. St. Petersburg: AANII. P. 10–13. [In Russian]

Kirpichnikov A.A. 1965. Some data on migrations of the south polar skua in East Antarctica. *Bulletin of Moscow Society of Naturalists* 70(5): 117–118. [In Russian]

Korotkevich E.S. 1958. Observations on birds during the first wintering of the Soviet Antarctic Expedition in 1956–1957. *Newsletter of the Soviet Antarctic Expedition* 3: 83–87. [In Russian]

Korotkevich E.S. 1959. The birds of East Antarctica. *Arctic and Antarctic Research* 1: 95–108. [In Russian]

Krietsch J., Esefeld J., Braun C., Lisovski S., Peter H.U. 2016. Long-term dataset reveals declines in breeding success and high fluctuations in the number of breeding pairs in two skua species breeding on King George Island. *Polar Biology* 39(4): 573–582. DOI: 10.1007/s00300-015-1808-7

Lindenmayer D.B., Likens G.E., Andersen A., Bowman D., Bull C.M., Burns E., Dickman C.R., Hoffmann A.A., Keith D.A., Liddell M.J., Lowe A.J., Metcalfe D.J., Phinn S.R., Russell-Smith J., Thurgate N., Wardle G.M. 2012. Value of long-term ecological studies. *Austral Ecology* 37(7): 745–757. DOI: 10.1111/j.1442-9993.2011.02351.x

Makushok V.M. 1959. About biological collections and observations in the Mirny observatory in 1958. *Newsletter of the Soviet Antarctic Expedition* 6: 40–42. [In Russian]

Mawson D. 1915. *The home of the blizzard: Being the story of the Australian Antarctic Expedition, 1911–1914*. Vol. 2. London: William Heinemann. 339 p.

Micol T., Jouventin P. 2001. Long-term population trends in seven Antarctic seabirds at Pointe Géologie (Terre Adélie) Human impact compared with environmental change. *Polar Biology* 24(3): 175–185. DOI: 10.1007/s003000000193

Mirny Observatory. 2020. *Federal Program «World Ocean» «Antarctic Research and Invastigation» Subprigran Russian Antarctic Expedition.* Available from http://www.aari.aq/stations/mir/mir_en.html

Mizin I.A. 2015. South polar skua *Catharacta maccormicki* near the station Mirny (Antarctica) in 2009–2010. *Russian Ornithological Journal* 24: 499–505. [In Russian]

Mizin Yu.A., Chernov A. 2000. *Report on the ecological and environmental research program conducted by 44th RAE at the Mirny Observatory*. Unpublished report. 25 p. [In Russian]

Norman F.I., Ward S.J. 1990. Foods of the south polar skua at Hop Island, Rauer Group, East Antarctica. *Polar Biology* 10(7): 489–493. DOI: 10.1007/bf00233696

Philippe-Lesaffre M., Thibault M., Caut S., Bourgeois K., Berr T., Ravache A., Vidal E., Courchamp F., Bonnaud E. 2023. Recovery of insular seabird populations years after rodent eradication. *Conservation Biology* 37(3): e14042. DOI: 10.1111/cobi.14042

Phillips R.A., Silk J.R.D., Massey A., Hughes K.A. 2019. Surveys reveal increasing and globally important populations of south polar skuas and Antarctic shags in Ryder Bay (Antarctic Peninsula). *Polar Biology* 42(2): 423–432. DOI: 10.1007/s00300-018-2432-0

Propp M.V. 1968. *Scuba diving in the Antarctic*. Leningrad: Hydrometeorological Publishing House. 265 p. [In Russian]

Pryor M.E. 1964. Adélie penguin and south polar skua of the Haswell Island. *Newsletter of the Soviet Antarctic Expedition* 49: 40–43. [In Russian]

Pryor M. 1965. Mortality of emperor penguin offspring (*Aptenodytes forsteri* Grey). *Arctic and Antarctic Research* 19: 54–61. [In Russian]

Pryor M.E. 1968. The avifauna of Haswell Island, Antarctica. *Antarctic Bird Studies* 12: 57–82. DOI: 10.1029/AR012P0057

Quintana R.D., Cirelli V., Orgeira J.L. 2000. Abundance and spatial distribution of bird populations at Cierva Point, Antarctic Peninsula. *Marine Ornithology* 28: 21–27.

Reif J. 2013. Long-term trends in bird populations: a review of patterns and potential drivers in North America and Europe. *Acta Ornithologica* 48(1): 1–16. DOI: 10.3161/000164513X669955

Reinhardt K., Hann S., Peter H.U., Wemhoff H. 2000. A review of the diets of Southern Hemisphere skuas. *Marine Ornithology* 28(1): 7–19.

Report. 1976. Report of the Eighth Antarctic Treaty Consultative Meeting, Oslo, 1975. *Polar Record* 18(113): 201–232. DOI: 10.1017/s003224740000022x

Ritz M.S., Millar C., Miller G.D., Phillips R.A., Ryan P., Sternkopf V., Liebers-Helbig D., Peter H.U. 2008. Phylogeography of the southern skua complex – rapid colonization of the southern hemisphere during a glacial period and reticulate evolution. *Molecular Phylogenetics and Evolution* 49(1): 292–303. DOI: 10.1016/j.ympev.2008.07.014

Sander M., Carneiro A.P.B., Balbao T.C., Bays S.R., Costa E.S., Mascarello N.E., Oliva T.D., Dos Santos C.R. 2005. Status and Trends of Antarctic Seabirds at Admiralty Bay, King George Island. *Polarforschung* 75(2–3): 145–150.

Shesterikov N.P. 1959. Brief characterization of fast ice in the Davis Sea (according to 1957 data). *Newsletter of the Soviet Antarctic Expedition* 5: 43–45. [In Russian]

Starck W. 1980. The avifauna of Haswell Island (East Antarctica) in summer of 1978/1979. *Polish Polar Research* 1(2–3): 183–195.

Syroechkovsky E.E. 1966. Ornithological observations in Antarctica and some questions of biogeography of the Antarctic land. In: *Antarctic. Reports of the Interdepartmental Commission for the Study of Antarctica for 1965*. Moscow. P. 103–129. [In Russian]

Taig-Johnston M., Strom M.K., Calhoun K., Nowak K., Ebensperger L.A., Hayes L. 2017. The ecological value of long-term studies of birds and mammals in Central America, South America and Antarctica. *Revista Chilena de Historia Natural* 90(1): 7. DOI: 10.1186/s40693-017-0070-5

Turner J., Marshall G.J., Clem K., Colwell S., Phillips T., Lu H. 2019. Antarctic temperature variability and change from station data. *International Journal of Climatology* 40(6): 2986–3007. DOI: 10.1002/joc.6378

Voronov P.S., Klimov L.V. 1960. Geological structure of the Mirny area. *Soviet Antarctic Expedition* 9: 185–196. [In Russian]

Wilson D.J., Lyver P.O.B., Greene T.C., Whitehead A.L., Dugger K.M., Karl B.J., Barringer J.R.F., McGarry R., Pollard A.M., Ainley D.G. 2017. South Polar Skua breeding populations in the Ross Sea assessed from demonstrated relationship with Adélie Penguin numbers. *Polar Biology* 40(3): 577–592. DOI: 10.1007/s00300-016-1980-4

Wilson K.J., Turney C., Fogwill C., Hunter J. 2015. Low numbers and apparent long-term stability of South Polar Skuas *Stercorarius maccormicki* at Commonwealth Bay, Antarctica. *Marine Ornithology* 43(1): 103–106.

Yudin K.A. 1958. Ornithological collections of the Soviet Antarctic Expedition (1955–1958). *Newsletter of the Soviet Antarctic Expedition* 3: 89–90. [In Russian]

МНОГОЛЕТНИЕ ИЗМЕНЕНИЯ ЧИСЛЕННОСТИ И ПРОСТРАНСТВЕННОГО РАСПРЕДЕЛЕНИЯ *STERCORARIUS MACCORMICKI* (STERCORARIIDAE, CHARADRIIFORMES) ОСТРОВОВ ХАСУЭЛЛ, ВОСТОЧНАЯ АНТАРКТИДА

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Долгосрочные исследования имеют решающее значение в экологии, оценке изменений окружающей среды, управлении природными ресурсами и сохранении биоразнообразия. *Stercorarius maccormicki* (далее южно-полярный поморник или поморник) – хищник, который может угрожать популяциям птиц из отрядов Sphenisciformes и Procellariiformes. Во многих регионах Антарктики тренды численности южно-полярного поморника неизвестны или не обновлялись. Это исследование представляет попытку ответа на вопрос, как реагировала локальная популяция южно-полярных поморников на изменения условий окружающей среды в течение исторического периода? Задачами исследования было (1) установить динамику численности размножающейся популяции южно-полярных поморников Хасуэлльских островов, острова Хасуэлл и мелких островов архипелага Хасуэлл в течение исторического периода (1956–2013 гг.) и (2) попытаться объяснить причины популяционных изменений. Второстепенный исследовательский вопрос был, имелись ли изменения пространственного распределения размножающейся популяции южно-полярного поморника на островах архипелага Хасуэлл в течение исторического периода? Исследования проводились на островах архипелага Хасуэлл (море Дейвиса, залив Трешникова, Южный океан) у побережья Антарктиды (Земля Королевы Мэри), в основном на территории особо охраняемого района Антарктики №127 «Остров Хасуэлл с прилегающей к нему колонией императорских пингвинов на припае». Наземный учет был основным методом определения размера птичьих колоний. Южно-полярные поморники размножались на 3–8 островах архипелага Хасуэлл. Они использовали весь диапазон высот суши для размещения гнезд. В исторический период популяция южно-полярных поморников архипелага Хасуэлл претерпевала изменения в условиях размножения. Снижение численности особей (-52%) наблюдалось между сезонами размножения 1956–1957 гг. и 1966–1967 гг. Между сезонами размножения 1966–1967 гг. и 1999–2000 гг. численность особей в популяции сократилась на 30.7% и достигла исторического минимума (18 размножающихся пар). Рост популяции на 344.4% был зафиксирован между сезонами размножения 1999–2000 гг. и 2009–2010 гг., увеличившись на 33.8% и достигнув исторического максимума (83 пары) в сезон размножения 2010–2011 гг. К сезону размножения 2012–2013 гг. популяция сократилась на 13.2%. На острове Хасуэлл между сезонами размножения 1956–1957 гг. и 2012–2013 гг. наблюдалось изменение численности особей южно-полярного поморника, аналогичное изменению общей численности размножающихся особей их популяции на архипелаге Хасуэлл в указанный выше период. Размножающаяся популяция южно-полярного поморника острова Хасуэлл вносит основной вклад в долговременную динамику численности особей вида. На малых островах архипелага Хасуэлл численность размножающихся южно-полярных поморников резко сократилась (-80%) между сезонами размножения 1956–1957 гг. и 1962–1963 гг. Сезоны размножения 1962–1963 гг., 1966–1967 гг. и 1999–2000 гг. характеризовались наиболее низкими показателями численности особей. В сезоны размножения с 1999–2000 гг. по 2009–2010 гг. численность особей поморника увеличилась на 400%. Уменьшение численности особей в популяции (-41.6%) произошло в период с 2009–2010 гг. по 2010–2011 гг. Затем последовало увеличение численности особей (на 36.3%) к сезону размножения 2012–2013 гг. На малых островах архипелага Хасуэлл численность особей поморника менялась независимо от изменения численности особей поморника на острове Хасуэлл (тест Манна-Уитни U = 48.5, p = 0.002 (асимптотическая (2-сторонняя))). В течение исторического периода изменение численности особей поморника архипелага Хасуэлл не зависело от изменений среднесуточной температуры ноября между сезонами размножения 1956–1957 гг. и 2012–2013 гг. (U = 0, p = 0.0017, n = 7 (асимптотическая (2-сторонняя))), когда у них происходила кладка яиц и их обогрев. Численность особей южно-полярного поморника в течение изучаемого периода изменялась независимо от изменений численности особей их кормовых ресурсов, *Aptenodytes forsteri*, *Pygoscelis adeliae* и *Fulmarus glacialoides* (соответственно, U = 49, p = 0.0006, n = 7; U = 16, p = 0.029, n = 4; U = 16, p = 0.029, n = 4 (асимптотическая (2-сторонняя))). Относительно высокая гибель яиц и птенцов в конкретный сезон размножения могли влиять на изменения численности особей в популяции поморника. Сиблинговая агрессия птенцов и локальные метеоусловия (усиление ветра, обильные осадки и резкие перепады поверхностных температур) конкретного сезона размножения также могли влиять на успех размножения поморников, что отложенным эффектом могло отражаться на долговременной динамике их размножающейся популяции. Деятельность человека влияла на популяцию поморника, но не исследовалась количественно. Причины исторических изменений обилия размножающихся особей в популяции южно-полярного поморника архипелага Хасуэлл остаются во многом не ясными.

Ключевые слова: деятельность человека, мониторинг, охрана, тенденция, тренд, численность, южно-полярный поморник

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IS THE GBIF APPROPRIATE FOR USE AS INPUT IN MODELS OF PREDICTING SPECIES DISTRIBUTIONS? STUDY FROM THE CZECH REPUBLIC

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Questions concerning species diversity have attracted ecologists and biogeographers for over a century, mainly because the diversity of life on Earth is in rapid decline, which is expected to continue in the future. One of the most important current database on species distribution data is the Global Biodiversity Information Facility (GBIF), which contains more than 2 billion occurrences for all organisms, and this number is continuously increasing with the addition of new data and by combining with other applications. Such data also exist in several national databases, most of which are unfortunately often not freely available and not included in GBIF. We suspected that the national databases, mostly professionally maintained by governmental organisations, may be more comprehensive than GBIF, which is not centrally organised and therefore the national databases may give more accurate predictions than GBIF. To test our assumptions, we have compared: (i) the amount of data included in the Czech database called Nálezová databáze ochrany přírody (NDOP, Discovery database of nature protection) with the amount of data in GBIF after its restriction to the Czech Republic, and (ii) the overlap of the predictions of species distributions for the Czech Republic, based on these two databases. We have used the family Orchidaceae as a model group. We found that: (i) there is a significantly larger number of records per studied region (Czech Republic) in NDOP, compared with GBIF, and (ii) the predictions of Maxent based on orchid records in NDOP are overlapping to a great degree with the predictions based on data based on orchid records in GBIF. Bearing in mind these results, we suggest that if only one database is available for the region studied, we must use this one. If more databases are available for the region studied, we should use the database containing most locations (usually some of the local ones, like NDOP), because using more locations implies larger significance of predictions of species distributions.

Key words: databases, Global Biodiversity Information Facility, NDOP, orchid distribution, species distribution models

Introduction

Questions concerning species diversity have attracted ecologists and biogeographers for over a century, mainly because the diversity of life on Earth is in rapid decline (Spooner et al., 2018; Baker et al., 2019; Halley & Pimm, 2023), which is expected to continue in the future (Román-Palacios & Wiens, 2020). For a reliable analysis of the rules governing the trends in species diversity, good data are necessary. To get them, direct sampling in the field, but also data available in museums and herbaria, which contain samples collected over centuries of field exploration (Smith & Blagoderov, 2012) are used. Mass digitalisation of all these data via interactive digital databases is now leading to their massive public availability (Maldonado et al., 2015) and to analyses using new computational methods and bioinformatic tools (Soberón & Peterson, 2004; Newbold, 2010).

Currently, one of the most important databases on species distribution data is the Global Biodiversity Information Facility (GBIF) (e.g. Beck et al., 2014; Maldonado et al., 2015; Chadin et al., 2017; Guedes et al., 2018; Alhajeri & Fourcade, 2019; Moudrý & Devillers, 2020; De Araujo et al., 2022), which contains currently more than 2 billion occurrences for all organisms, and this number is continuously increasing with the addition of new data and by combining with other applications (e.g. iNaturalist.org). Similar kind of data also exists in some national databases, such as the Czech database called Nálezová databáze ochrany přírody (NDOP, Discovery database of nature protection; see https://portal.nature.cz/nd/), most of which are unfortunately often not freely available and not included in the GBIF.

Thanks to the availability of powerful computers and advanced software, the occurrence and distribution of threatened species is now determined by species distribution models (SDMs) in combination with GIS techniques, which use the above-mentioned databases of species occurrence records and environmental data on climate, land use, geological substrate and other parameters as inputs (e.g. Guisan & Thuiller, 2005; Elith & Leathwick, 2009; Jiang & Purvis, 2023). Based on these, numerous papers have been published on current and future potential distributions of many species, and their range shifts under various climate change scenarios (e.g. Kistner & Hatfield, 2018; Weterings & Vetter, 2018; Tsiftsis & Djordjević, 2020; Namkhan et al., 2022; Arotolu et al., 2023). Many of them have used GBIF as input (e.g. Salvà-Catarineu et al., 2021; Daba et al., 2023; Krapf, 2023; Mallen-Cooper et al., 2023).

We have used the family Orchidaceae as a model group. Orchidaceae have a great species richness with about 20 000–35 000 species (Dressler, 1993; Chase et al., 2003; Cribb et al., 2003; Christenhusz & Byng, 2016). They are heavily threatened by extinction, and dispose of many varieties of reproductive strategies (Steffelová et al., 2023) and have an extremely restricted distribution with relatively small populations (Švecová et al., 2023). These traits make orchids an ideal model group because they are (i) important in conservation biology (Pillon & Chase, 2007; Swarts & Dixon, 2009) and (ii) crucial for their distribution and conservation status (Zhang et al., 2015).

We suspected that on the local scale the national databases, mostly professionally maintained by governmental organisations, may be more comprehensive than GBIF, managed by the GBIF Secretariat including four groups, so it is not centrally organised and therefore the national databases may give more accurate predictions than GBIF. To our knowledge, no study was yet published comparing the outcomes of any SDM method by using data from GBIF with those using any other national database. To test our expectations, we have compared (i) the amount of data included in the Czech database NDOP with the amount of data in GBIF, when it is restricted to the Czech Republic, and (ii) the overlap of the predictions of species distributions for the Czech Republic based on these two databases.

Material and Methods

The Czech Republic was chosen as a model country because its orchid flora is very well studied (Štípková et al., 2021). It is covered mainly by highlands of moderate altitude and higher mountains occur at its borders, especially in the north and south. The climate of the Czech Republic is typically temperate with cold, cloudy winters and hot summers. However, there are some regional and local differences due to the relief that forms a complex topography in this area (Palacký University Olomouc, 2020). Because the Czech Republic is a relatively small country in terms of latitudinal range, temperature and precipitation are mostly affected by local heterogeneity and altitude (Štípková et al., 2020b).

Two databases were compared: (i) one of the most important current database on species distribution data, the Global Biodiversity Information Facility (GBIF), which is freely accessible on https://www.gbif.org/ and (ii) the database NDOP (https://portal.nature.cz/nd/) of the Nature Conservation Agency of the Czech Republic, which is unavailable to the public to preserve orchid localities in the country. We used 55 orchid taxa. Their classification and nomenclature follow Danihelka et al. (2012). All studied species are threatened and protected on the national level and included on the national Red List (Grulich & Chobot, 2017).

NDOP was chosen because we have enough experience with it. Previously, Štípková & Kindlmann (2015), Štípková et al. (2018, 2020a) worked on the revision of orchid records in 24 mapping squares (see the network of mapping squares used for these purposes on https://www.entospol.cz/sit-mapovych-ctvercu/) in South Bohemia based on NDOP. More than 82% of records included in these squares were confirmed in NDOP, when revised. It was therefore supposed that records included in NDOP would be similarly correct for the whole Czech Republic with a small number of errors. Thus, we considered the NDOP to be sufficiently reliable for the purpose of this study. Nature Conservation Agency is divided into many regional branches across the whole area of the Czech Republic and each branch manages a certain area of the country. All data from the regional branches are then centralised in one database that guarantees uniformity of the database records. Moreover, NDOP allows their users to easily provide feedback on specific records, whereas GBIF does not.

We used Maxent (Phillips et al., 2006; Phillips & Dudík, 2008; Elith et al., 2011) to predict the current potential distribution of orchid species in the Czech Republic. The maximum entropy algorithm in the Maxent application (Phillips et al., 2006; Phillips & Dudík, 2008; Elith et al., 2011) is used for modelling species distribution from presence-only species records (Elith et al., 2011). This approach is widely used for predicting current as well as future distributions of species from a set of occurrence records and environmental variables (Yi et al., 2016; Tsiftsis & Djordjević, 2020). A great advantage of this method is that it has a high predictive performance even for very small sample sizes (Hernandez et al., 2006; Elith & Leathwick, 2009; David et al., 2020).

Bioclimatic variables and map of geological substrates of the Czech Republic were used as environmental predictors in the SDMs. Initially, 21 environmental variables were selected as predictors. Nineteen of them were bioclimatic variables and the remaining two were altitude and geological substrate. The bioclimatic variables were obtained from the WorldClim database (Fick & Hijmans, 2017) in a 30-sec resolution (approximately 1 km^2). The map of geological substrate was obtained from the geological map of the Czech Republic based on the digital geological map 1:500 000 (Czech Geological Survey, 1998). Because the map of the geological substrate is in vector format, the layer was converted into a raster format at the same resolution and extent with the layers of the bioclimatic variables.

To account for multicollinearity between the 19 bioclimatic variables and avoid overfitting, Pearson correlation coefficients were calculated for all pairwise interactions. To eliminate highly correlated variables, only one (i.e. the one with the higher percent contribution and training gain) was selected among any pair of those with a correlation coefficient r in the range $|r| > 0.70$. Specifically, in modelling the potential distribution of the studied species, the non-highly intercorrelated bioclimatic variables were used BIO 01 (annual mean temperature), BIO 02 (mean diurnal temperature range), BIO 05 (maximal temperature of warmest month), BIO 09 (mean temperature of driest quarter), BIO 12 (annual precipitation), and BIO 15 (precipitation seasonality). In addition, the altitude and the geological substrate were also used. The geological map of the Czech Republic contains the only categorial variable used in the models, but we treated all geological categories as dummy variables.

For both databases (NDOP and GBIF), we removed duplicate records (records falling in the same 1 km^2 grid cell), and we ran Maxent models only for species having at least 12 records in both databases. For each orchid species and database used, ten models were run. At each run, species records were randomly divided into training and testing datasets using the ratio between 80% and 20%, and we used 10 000 background samples to characterise the environmental conditions of the area of interest. Based on the output of the ten replicates, we calculated the average prediction.

SDMs outputs are numerical predictions, which provide a measure of the habitat suitability in an area (for example, at a country level). To convert these maps into presence/absence (binary) maps, the Maximum Sensitivity plus Specificity (MaxSSS) threshold was applied for each orchid species and database. This threshold was selected, as it provides better results than other thresholds, independently of the data used either presence/absence or presence-only data (Liu et al., 2016).

A niche equivalency test was used that shows Schoener's D and Hellinger Distances I of niche overlap (Warren et al., 2008). These statistics use suitability scores and have been widely used previously (e.g. Nunes & Pearson, 2017; Martínez-Méndez et al., 2019). Both these variables (D and I) measure niche overlap using different calculations, and their values range from 0 (no overlap between the two distributions) to 1 (identical distributions). Only D statistic was used for comparisons of percentage niche overlap of orchid occurrence data using Maxent model, as it is widely used in pairwise comparisons (e.g. El-Gabbas & Dormann, 2018; Chevalier et al., 2022).

To examine, whether there are significant differences in the mean altitude of the distribution of each of the studied species, we extracted the altitude values of the grid cells where each orchid is potentially present after converting the habitat suitability values into presence/

absence data. Thus, we compared the altitudinal values of the species distributions between the predictions of the two different datasets used in Maxent by using the Mann-Whitney U test in R v. 4.1.2 (R Core Team, 2023).

Results

In total, 31 orchid taxa had more than 12 records in both databases after removing the duplicates (Table 1). The number of orchid records included in GBIF and NDOP differed to a great degree, when compared in the region of the whole Czech Republic (Fig. 1). Initially, GBIF database contained 4328 of orchid records, NDOP contained 105 810 orchid records. The number of grid cell records analysed here, i.e. those containing enough records, after the reduction for duplicates etc., ranged from 61 (*Neotinea tridentata* (Scop.) R. M. Bateman, Pridgeon & M. W. Chase) to 13 636 records (*Dactylorhiza majalis* (Rchb.) P. F. Hunt & Summerh.) in the NDOP database, and from 13 (*Gymnadenia densiflora* (Wahlenb.) A. Dietr.) to 384 (*Neottia ovata* (L.) R. Br.) records in the GBIF database (Table 1).

Table 1. Species records used in Maxent and *D* statistics showing the niche overlap between the predictions of the two databases considered of 31 orchid taxa of the Czech Republic using Maxent

Species	Number of species records		Maxent
	NDOP	GBIF	*D* statistics
Anacamptis morio (L.) R.M.Bateman, Pridgeon & M.W.Chase	927	115	0.790
Anacamptis pyramidalis (L.) Rich.	238	63	0.625
Cephalanthera damasonium (Mill.) Druce	3631	322	0.860
Cephalanthera longifolia (L.) Fritsch	1493	244	0.813
Cephalanthera rubra (L.) Rich.	542	48	0.698
Cypripedium calceolus L.	576	95	0.692
Dactylorhiza fuchsii (Druce) Soó	4912	143	0.754
Dactylorhiza incarnata (L.) Soó	397	51	0.667
Dactylorhiza maculata (L.) Soó	346	32	0.711
Dactylorhiza majalis (Rchb.) P.F.Hunt & Summerh.	13 636	233	0.867
Dactylorhiza sambucina (L.) Soó	1150	92	0.751
Epipactis atrorubens (Hoffm.) Besser	643	85	0.700
Epipactis helleborine (L.) Crantz	7109	259	0.866
Epipactis palustris (L.) Crantz	1363	91	0.775
Gymnadenia conopsea (L.) R.Br.	2254	76	0.765
Gymnadenia densiflora (Wahlenb.) A.Dietr.	306	13	0.549
Neotinea tridentata (Scop.) R.M.Bateman, Pridgeon & M.W.Chase	61	19	0.455
Neotinea ustulata (L.) R.M.Bateman, Pridgeon & M.W.Chase	1082	70	0.813
Neottia cordata (L.) Rich.	369	22	0.749
Neottia nidus-avis (L.) Rich.	4867	272	0.848
Neottia ovata (L.) Hartm.	5121	384	0.867
Ophrys apifera Huds.	99	31	0.533
Ophrys insectifera L.	121	30	0.501
Orchis mascula (L.) L.	3845	83	0.737
Orchis militaris L.	709	135	0.796
Orchis pallens L.	598	163	0.779
Orchis purpurea Huds.	478	349	0.765
Platanthera bifolia (L.) Rich.	6104	255	0.837
Platanthera chlorantha (Custer) Rchb.	2113	37	0.815
Spiranthes spiralis (L.) Chevall.	232	16	0.729
Traunsteinera globosa (L.) Rchb.	619	42	0.609

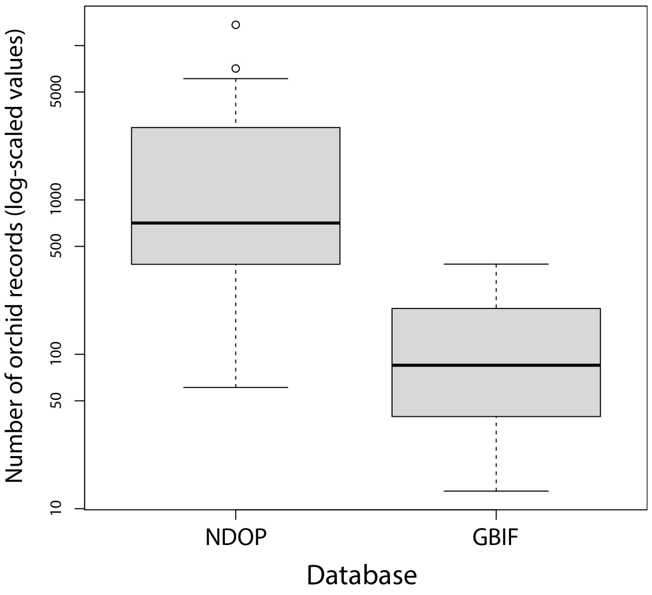

Fig. 1. Boxplot showing the number of orchid records (after removing duplicate records) in both databases (NDOP and GBIF) in the Czech Republic.

The values of the *D* statistics indicating the degree of niche overlap are presented in Table 1. The lowest niche overlap was observed in *Neotinea tridentata* (*D* value is 0.455), whereas the highest niche overlap was found in *Dactylorhiza majalis* and *Neottia ovata* (*D* value of both is 0.867). Most species showed a percentage overlap between 70% and 80%, but no species reached a percentage overlap between 90% and 100% (Fig. 2). Habitat suitability maps for each species based on data from the GBIF database and NDOP database are presented in Electronic Supplement 1. They show that GBIF often (but not always!) makes similar predictions to those made by NDOP.

The Mann-Whitney U test revealed significant altitudinal differences between data predictions from the NDOP and GBIF databases after Maxent had been applied (Table 2). Almost all data predictions of NDOP were significantly different from those of the GBIF database ($p < 0.001$). Only for *Spiranthes spiralis* (L.) Chevall. the *p*-value was lower ($p < 0.05$). The differences were not statistically significant only for two species, namely *Gymnadenia conopsea* (L.) R. Brown. and *Traunsteinera globosa* (L.) Rchb. The predictions of the Maxent model revealed statistically higher altitudinal distribution (in terms of the higher mean altitude) for 20 out of 31 studied species.

Table 2. Comparison of data presented in the NDOP and GBIF databases after Maxent predictions using Mann-Whitney U test in the Czech Republic

Species	Number of presence grid cells after Maxent predictions		Altitudinal statistics of the presence grid cells obtained through Maxent model using NDOP data				Altitudinal statistics of the presence grid cells obtained through Maxent model using GBIF data				Mann-Whitney U test between data of NDOP and GBIF
	NDOP	GBIF	Min	Max	Mean	SD	Min	Max	Mean	SD	
Anacamptis morio	15 867	30 444	183	866	447.01	124.68	187	699	397.17	88.95	**
Anacamptis pyramidalis	10 383	7460	162	841	423.56	128.64	162	656	376.06	86.39	**
Cephalanthera damasonium	37 059	46 600	86	671	356.33	94.41	131	598	323.52	84.06	**
Cephalanthera longifolia	23 313	26 284	200	841	420.34	98.67	187	1359	403.30	105.56	**
Cephalanthera rubra	21 286	20 198	97	825	415.48	87.41	245	745	423.81	74.78	**
Cypripedium calceolus	28 840	50 398	180	690	370.70	91.64	51	577	298.18	77.66	**
Dactylorhiza fuchsii	20 551	15 897	289	1524	721.20	186.47	157	1524	761.42	193.02	**
Dactylorhiza incarnata	32 281	27 520	51	1007	302.94	123.37	51	1524	277.10	115.65	**
Dactylorhiza maculata	23 650	10 966	223	1524	654.78	218.79	185	1524	806.85	212.42	**
Dactylorhiza majalis	47 016	36 189	382	1402	638.53	142.23	157	1461	637.57	190.93	**
Dactylorhiza sambucina	6179	9341	271	982	528.45	147.00	296	1407	646.23	195.12	**
Epipactis atrorubens	25 068	14 465	177	1248	492.41	188.78	235	1524	718.49	232.75	**
Epipactis helleborine	43 931	24 665	148	1461	517.68	205.98	235	1524	651.44	219.08	**
Epipactis palustris	24 220	25 905	159	1080	477.55	163.07	125	928	357.45	130.59	**
Gymnadenia conopsea	16 199	8385	183	1524	604.26	221.12	125	1524	622.69	244.74	0.168
Gymnadenia densiflora	14 816	43 087	125	1461	393.75	146.58	51	516	281.40	77.67	**
Neotinea tridentata	19 116	35 078	168	827	343.50	124.34	51	516	258.34	72.80	**
Neotinea ustulata	20 544	22 946	51	729	410.17	105.60	51	656	364.54	104.50	**
Neottia cordata	13 008	5154	288	1524	819.48	152.36	742	1524	953.35	131.51	**
Neottia nidus-avis	30 649	31 391	162	866	395.92	104.79	189	785	364.61	86.69	**
Neottia ovata	35 841	31 233	125	1325	446.99	184.64	125	1325	386.59	182.54	**
Ophrys apifera	13 701	21 397	162	671	343.17	105.90	134	545	274.90	86.71	**
Ophrys insectifera	18 257	5340	51	906	361.74	175.65	51	863	299.98	96.65	**
Orchis mascula	8705	8791	249	969	528.73	145.60	237	857	492.85	127.91	**
Orchis militaris	11 695	12 880	152	779	327.19	119.01	51	1524	304.25	124.16	**
Orchis pallens	9638	12 834	175	733	412.72	108.13	192	671	380.36	106.62	**
Orchis purpurea	28 813	22 468	86	623	333.34	84.03	86	559	285.07	68.93	**
Platanthera bifolia	44 770	29 432	189	1209	494.24	174.18	230	1461	553.56	217.43	**
Platanthera chlorantha	35 793	13 703	162	1282	581.17	210.81	51	1524	740.47	270.59	**
Spiranthes spiralis	32 768	92 074	122	1209	425.56	109.94	143	1133	420.58	143.28	*
Traunsteinera globosa	6289	3738	171	1461	537.32	185.68	171	952	521.89	142.36	0.182

Note: ** – $p < 0.001$, * – $p < 0.05$.

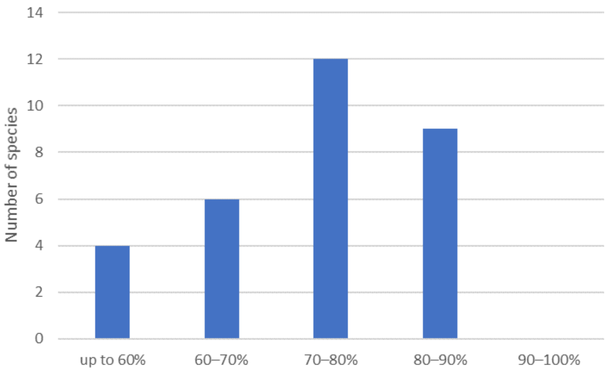

Fig. 2. Percentage overlap between data from NDOP and GBIF database using *D* statistic from Maxent application in the Czech Republic.

Fig. 3 shows the importance of the environmental variables when orchid records from NDOP and GBIF are used in Maxent. The evaluation of the importance of each environmental variable was based on the jackknife test using each predictor separately. The lengths of the bars correspond to the percentage contribution of each environmental predictor to the total training gain of each model. For example, in the line associated with *Anacamptis morio* (L.) R. M. Bateman, Pridgeon & M. W. Chase, when NDOP data are used, the longest bar (the dark green one) is the mean diurnal temperature range (BIO 02). This means that the most important environmental variable for *Anacamptis morio*, when NDOP data are used, is the mean diurnal temperature range (BIO 02). Another important output of Fig. 3 is that the importance of variables may vary to a great extent between various databases used in the Maxent model. Specifically, for *Gymnadenia densiflora*, the geological substrate was the most important variable when data from NDOP were used, whereas altitude was among the less important ones. On the contrary, when the GBIF data were used, the importance of altitude was high, whereas that of the geological substrate was not. Something similar was also observed in the case of *Spiranthes spiralis*: when NDOP data were used, variables had a rather equal importance in the model, whereas when GBIF data were used, precipitation seasonality (BIO 15) was by far the most important variable compared to the others.

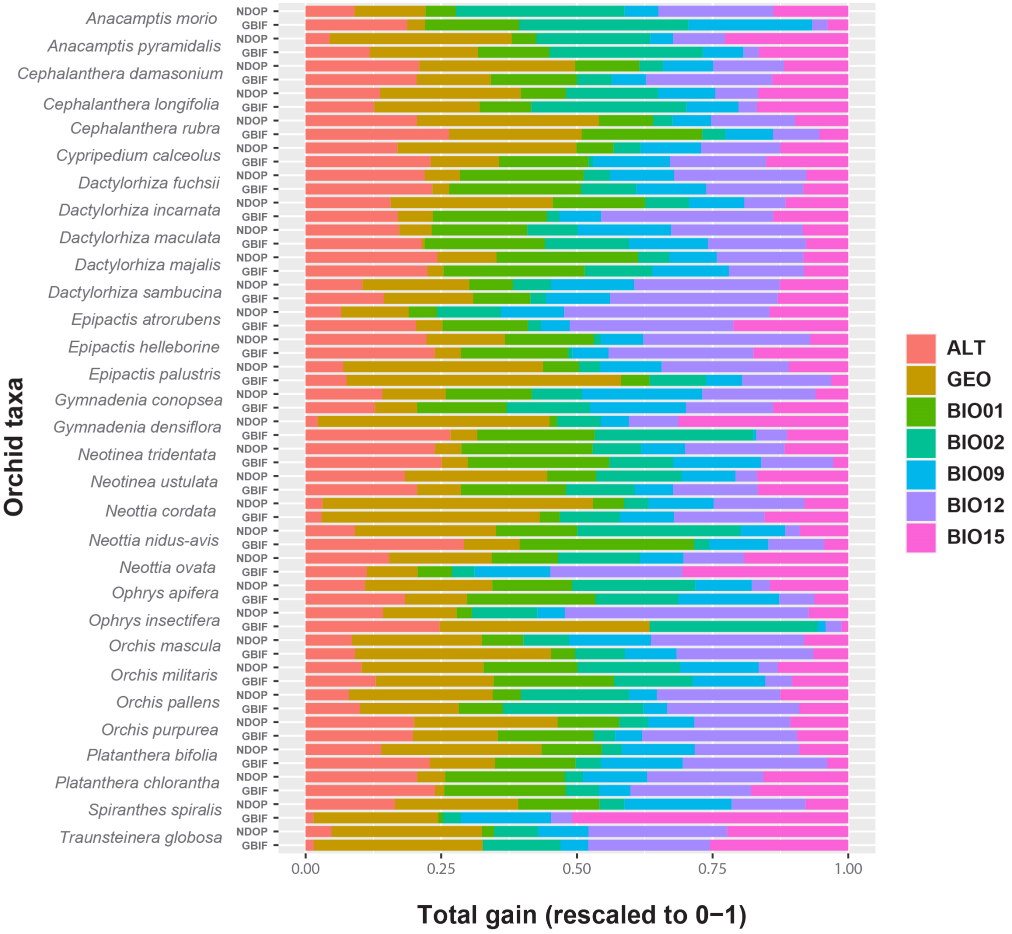

Fig. 3. The importance of the variables when orchid records from NDOP and GBIF are used in Maxent in the Czech Republic. The evaluation of the importance of each environmental variable was based on the jackknife test using each predictor separately. The lengths of the bars correspond to the percentage contribution of each environmental predictor to the total training gain of each model. Designation of the variables: ALT (altitude), GEO (geology), BIO 01 (annual mean temperature), BIO 02 (mean diurnal temperature range), BIO 09 (mean temperature of driest quarter), BIO 12 (annual precipitation) and BIO 15 (precipitation seasonality).

Differences in importance of the corresponding variables for the 31 orchid taxa when NDOP vs. GBIF data were used are documented in scatterplots in Fig. 4. The importance of altitude (ALT) and annual mean temperature (BIO 01) was higher (points above the diagonal in Fig. 4) when GBIF data were used, compared to the results of the NDOP data. On the contrary, when the NDOP data were used, the importance of the geological substrate for most orchid taxa was much stronger than when GBIF data were used (points below the diagonal in Fig. 4).

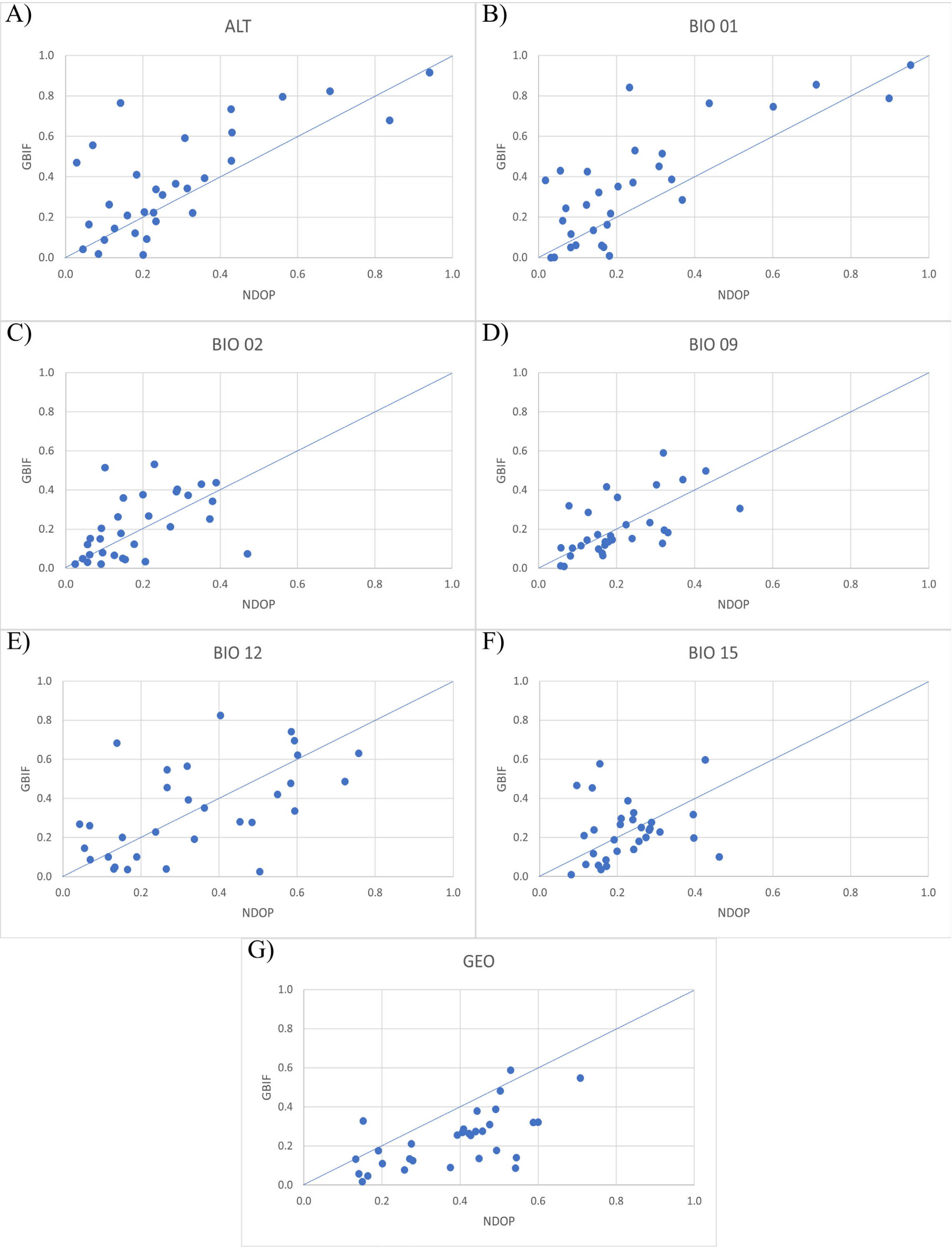

Fig. 4. Scatterplots showing the importance of each environmental variable based on the jack-knife test using each predictor separately in the case of the NDOP and GBIF database in the Czech Republic. Points above the main diagonal indicate a higher importance of the corresponding variable, when GBIF data are used and vice versa. Designation of the variables: A) ALT (altitude), B) BIO 01 (annual mean temperature), C) BIO 02 (mean diurnal temperature range), D) BIO 09 (mean temperature of driest quarter), E) BIO 12 (annual precipitation), F) BIO 15 (precipitation seasonality) and G) GEO (geology). Each dot represents an individual orchid species.

Discussion

The central topic of this paper is the comparison of accuracy of predictions based on public databases like GBIF against the governmentally controlled ones, like NDOP. We must admit that there are some practical advantages, when public databases, such as GBIF, are used for saving time and money and the uniformity of presented data that are ready to use for many analyses (Maldonado et al., 2015). However, how do the resulting predictions differ? What are the problems, when predictions based on records in the public databases like GBIF are compared with predictions of governmentally maintained ones, like NDOP?

First, our results show that there is a much larger number of orchid records in the governmentally maintained databases like NDOP than in public ones like GBIF, when like with like (i.e. records for the same region in both databases) is compared. In our study, the number of orchid records included in NDOP in the region specified at the beginning of the analysis (Czech Republic in this case) was much higher than that in GBIF (see Table 1). The reason for this is the long-term and systematic collection of data for NDOP from various parts of the Czech Republic. This renders a great advantage to the NDOP database for accuracy of predictions of species distribution in the region selected. The prevalence of records in the governmentally maintained databases, as opposed to the public ones, when like with like (the same region for both databases) is considered is not a solitary phenomenon of the Czech Republic. For example, the same occurs, when Greece is considered: GBIF for Greece has about 25 000 records (https://www.gbif.org/analytics/global), whereas the national database owned by Dr. Spyros Tsiftsis has more than 170 000 records (personal communication). So, the prevalence of records in the governmentally maintained databases, as opposed to the public ones, when like with like (the same region for both databases) is considered, seems to be a general phenomenon, if the governmentally maintained databases are good.

Second, in public databases like GBIF, the records are usually not as strictly controlled for correctness as governmentally maintained databases like NDOP. Questionable quality of unverified datasets, mistakes in the taxonomic identification of specimens or inaccurate georeferencing are common traits of public databases (Maldonado et al., 2015). Scientists and experts agree that a correct species name should be a minimum requirement for including the data in public databases, as well as an accurate georeferencing (Marcer et al., 2022), but this is not always the case. Mistakes in taxonomic identification can often be corrected by a taxonomist who has the possibility to access the specimen personally or at least see its image (Maldonado et al., 2015), and this is much more common in governmentally maintained databases like NDOP than in GBIF. A similar situation is with the errors in georeferencing (Graham et al., 2004).

Third, there is a common problem with records in public databases, like GBIF. Here, there are data spatially biased in most cases, which can greatly affect results of macroecological/biogeographical studies (Beck et al., 2014; Bowler et al., 2022; Boyd et al., 2022).

All these problematic inaccuracies can (and often will) affect results of studies dealing with biodiversity patterns, environmental niches and/or distribution predictions. Thus, information from public databases, like GBIF, must be used with caution due to important issues with data quality mentioned in the previous three paragraphs (Bowler et al., 2022; Boyd et al., 2022; Marcer et al., 2022). Just one example: it is well known that orchid distribution is strongly affected by the geological substrate (Djordjević & Tsiftsis, 2022). This is obvious when NDOP records, but not when the GBIF records are used (see Fig. 4G).

Surprisingly, despite of what was said in the four previous paragraphs, when two predictions were made: one based on records contained in NDOP and another one based on records contained in GBIF, then these two predictions were overlapping to a great degree in most cases (Table 1; Fig. 2), and there were often only rather small differences between them (Table 2; Fig. 4). Also, our results in Electronic Supplement 1 show that GBIF often (but not always!) makes similar predictions as NDOP. This suggests that GBIF may be used (with caution!) when no good local database is available.

No matter of what was said above here in the Discussion, there is one criterion that should be used, if the mentioned above does not suggest any preference for the use of public or governmentally based database: it is well known in statistics that the significance of the tests is positively correlated with the amount of data used in the test (Sokal & Rohlf, 2012). Therefore, the database containing more locations in the region considered should be preferred, because more locations imply a larger significance of predictions of species distribution.

Conclusions

Our analyses have shown that the predictions of species distributions based on data of orchid records from NDOP and GBIF databases are overlapping to a great degree. NDOP allows their users to easily provide feedback on specific records, whereas GBIF does not. Problematic inaccuracies might affect results of studies dealing with biodiversity patterns, environmental niches and/or distribution predictions, when based on public databases like GBIF, which therefore must be considered with caution. However, public databases have advantages in saving time and money in data collection and in uniformity of these data. With respect to significance of tests used, we suggest always using the database containing more locations (NDOP in our case), because more locations imply larger significance of predictions of species distributions.

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Supporting Information

Habitat suitability maps of orchid species in the Czech Republic may be found in the **Supporting Information**.

References

Alhajeri B.H., Fourcade Y. 2019. High correlation between species-level environmental data estimates extracted from IUCN expert range maps and from GBIF occurrence data. *Journal of Biogeography* 46(7): 1329–1341. DOI: 10.1111/jbi.13619

Arotolu T.E., Wang H.N., Lv J.N., Shi K., Huang L.Y., Wang X.L. 2023. Modeling the current and future distribution of Brucellosis under climate change scenarios in Qinghai Lake basin, China. *Acta Veterinaria-Beograd* 73(3): 325–345. DOI: 10.2478/acve-2023-0025

Baker D.J., Clarke R.H., McGeoch M.A. 2019. The power to detect regional declines in common bird populations using continental monitoring data. *Ecological Applications* 29(5): e01918. DOI: 10.1002/eap.1918

Beck J., Böller M., Erhardt A., Schwanghart W. 2014. Spatial bias in the GBIF database and its effect on modeling species' geographic distributions. *Ecological Informatics* 19: 10–15. DOI: 10.1016/j.ecoinf.2013.11.002

Bowler D.E., Callaghan C.T., Bhandari N., Henle K., Barth B.M., Koppitz C., Klenke R., Winter M., Jansen F., Bruelheide H., Bonn A. 2022. Temporal Trends in the Spatial Bias of Species Occurrence Records. *Ecography* 2022(8): e06219. DOI: 10.1111/ecog.06219

Boyd R.J., Aizen M.A., Barahona-Segovia R.M., Flores-Prado L., Fontúrbel F.E., Francoy T.M., Lopez-Aliste M., Martinez L., Morales C.L., Ollerton J., Pescott O.L., Powney G.D., Saraiva A.M., Schmucki R., Zattara E.E., Carvell C. 2022. Inferring trends in pollinator distributions across the Neotropics from publicly available data remains challenging despite mobilization efforts. *Diversity and Distributions* 28(7): 1404–1415. DOI: 10.1111/ddi.13551

Chadin I., Dalke I., Zakhozhiy I., Malyshev R., Madi E., Kuzivanova O., Kirillov D., Elsakov V. 2017. Distribution of the invasive plant species *Heracleum sosnowskyi* Manden. in the Komi Republic (Russia). *Phytokeys* 77: 71–80. DOI: 10.3897/phytokeys.77.11186

Chase M.W., Cameron K.M., Barrett R.L., Freudebstein J.V. 2003. DNA data and Orchidaceae systematics: A new phylogenetic classification. In: K.W. Dixon, S.P. Kell, R.L. Barrett, P.J. Cribb (Eds.): *Orchid Conservation.* Kota Kinabalu: Natural History Publications (Borneo). P. 69–89.

Chevalier M., Zarzo-Arias A., Guélat J., Mateo R.G., Guisan A. 2022. Accounting for niche truncation to improve spatial and temporal predictions of species distributions. *Frontiers in Ecology and Evolution* 10: 944116. DOI: 10.3389/fevo.2022.944116

Christenhusz M.J.M., Byng J.W. 2016. The number of known plants species in the world and its annual increase. *Phytotaxa* 261(3): 201–217. DOI: 10.11646/phytotaxa.261.3.1

Cribb P.J., Kell S.P., Dixon K.W., Barrett R.L. 2003. Orchid conservation: A global perspective. In: K.W. Dixon, S.P. Kell, R.L. Barrett, P.J. Cribb (Eds.): *Orchid Conservation.* Kota Kinabalu: Natural History Publications (Borneo). P. 1–2.

Czech Geological Survey. 1998. *Geological map of the Czech Republic 1:500 000 (GEOCR500).* Available from https://micka.geology.cz/en/record/basic/5f5b4530-a87c-4bf3-b45a-57d30a010852

Daba D., Kagnew B., Tefera B., Nemomissa S. 2023. Modelling the current and future distribution potential areas of *Peperomia abyssinica* Miq., and *Helichrysum citrispinum* Steud. ex A. Rich. in Ethiopia. *BMC Ecology and Evolution* 23(1): 71. DOI: 10.1186/s12862-023-02177-z

Danihelka J., Chrtek J.J., Kaplan Z. 2012. Checklist of vascular plants of the Czech Republic. *Preslia* 84: 647–811.

David O.A., Akomolafe G.F., Onwusiri K.C., Fabolude G.O. 2020. Predicting the distribution of the invasive species *Hyptis suaveolens* in Nigeria. *European Journal of Environmental Sciences* 10(2): 98–106. DOI: 10.14712/23361964.2020.11

De Araujo M.L., Quaresma A.C., Ramos F.N. 2022. GBIF information is not enough: national database improves the inventory completeness of Amazonian epiphytes. *Biodiversity and Conservation* 31(11): 2797–2815. DOI: 10.1007/s10531-022-02458-x

Djordjević V., Tsiftsis S. 2022. The role of ecological factors in distribution and abundance of terrestrial orchids. In: J.M. Mérillon, H. Kodja (Eds.): *Orchids Phytochemistry, Biology and Horticulture*. Cham: Springer Nature. P. 1–71. DOI: 10.1007/978-3-030-11257-8_4-1

Dressler R.L. 1993. *Phylogeny and Classification of the Orchid Family*. Cambridge: Cambridge University Press. 301 p.

El-Gabbas A., Dormann C.F. 2018. Wrong, but useful: regional species distribution models may not be improved by range-wide data under biased sampling. *Ecology and Evolution* 8(4): 2196–2206. DOI: 10.1002/ece3.3834

Elith J., Leathwick J. 2009. The contribution of species distribution modelling to conservation prioritization. In: A. Moilanen, A.K. Wilson, H.P. Possingham (Eds.): *Spatial conservation prioritization. Quantitative methods and computational tools*. New York: Oxford University Press Inc. P. 70–93.

Elith J., Phillips S.J., Hastie T., Dudík M., Chee Y.E., Yates C.J. 2011. A statistical explanation of MaxEnt for ecologist. *Diversity and Distributions* 17(1): 43–57. DOI: 10.1111/j.1472-4642.2010.00725.x

Fick S.E., Hijmans R.J. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37(12): 4302–4315. DOI: 10.1002/joc.5086

Graham C.H., Ferrier S., Huettman F., Moritz C., Peterson A.T. 2004. New developments in museum-based informatics and applications in biodiversity analysis. *Trends in Ecology and Evolution* 19(9): 497–503. DOI: 10.1016/j.tree.2004.07.006

Grulich V., Chobot K. 2017. Red list of threatened species of the Czech Republic vascular plants. *Příroda* 35: 1–178.

Guedes T.B., Sawaya R.J., Zizka A., Laffan S., Faurby S., Pyron R.A., Bérnils R.S., Jansen M., Passos P., Prudente A.L.C., Cisneros-Heredia D.F., Braz H.B., Nogueira C.D., Antonelli A. 2018. Patterns, biases and prospects in the distribution and diversity of Neotropical snakes. *Global Ecology and Biogeography* 27(1): 14–21. DOI: 10.1111/geb.12679

Guisan A., Thuiller W. 2005. Predicting species distribution: Offering more than simple habitat models. *Ecology Letters* 8(9): 993–1009. DOI: 10.1111/j.1461-0248.2005.00792.x

Halley J.M., Pimm S.L. 2023. The rate of species extinction in declining or fragmented ecological communities. *PloS ONE* 18(7): e0285945. DOI: 10.1371/journal.pone.0285945

Hernandez P.A., Graham C.H., Master L.L., Albert D.L. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29(5): 773–785. DOI: 10.1111/j.0906-7590.2006.04700.x

Jiang Y., Purvis A. 2023. How land use affects biodiversity: an analysis of the differences in the effects recorded on different continents. *European Journal of Environmental Sciences* 13(1): 15–22. DOI: 10.14712/23361964.2023.2

Kistner E.J., Hatfield J.L. 2018. Potential geographic distribution of Palmer Amaranth under current and future climates. *Agricultural and Environmental Letters* 3(1): 170044. DOI: 10.2134/ael2017.12.0044

Krapf P. 2023. Contribution of the public to the modelling of the distributions of species: Occurrence and current and potential distribution of the ant *Manica rubida* (Hymenoptera: Formicidae). *European Journal of Entomology* 120: 137–148. DOI: 10.14411/eje.2023.017

Liu C., Newell G., White M. 2016. On the selection of thresholds for predicting species occurrence with presence-only data. *Ecology and Evolution* 6(1): 337–348. DOI: 10.1002/ece3.1878

Maldonado C., Molina C.I., Zizka A., Persson C., Taylor C.M., Albán J., Chilquillo E., Rønsted N., Antonelli A. 2015. Estimating species diversity and distribution in the era of Big Data: to what extent can we trust public databases?. *Global Ecology and Biogeography* 24(8): 973–984. DOI: 10.1111/geb.12326

Mallen-Cooper M., Rodríguez-Caballero E., Eldridge D.J., Weber B., Büdel B., Höhne H., Cornwell W.K. 2023. Towards an understanding of future range shifts in lichens and mosses under climate change. *Journal of Biogeography* 50(2): 406–417. DOI: 10.1111/jbi.14542

Marcer A., Chapman A.D., Wieczorek J.R., Picó F.X., Uribe F., Waller J., Ariño A.H. 2022. Uncertainty matters: Ascertaining where specimens in natural history collections come from and its implications for predicting species distributions. *Ecography* 2022(9): e06025. DOI: 10.1111/ecog.06025

Martínez-Méndez N., Mejía O., Ortega J., Méndez-de la Cruz F. 2019. Climatic niche evolution in the viviparous *Sceloporus torquatus* group (Squamata: Phrynosomatidae). *PeerJ* 6: e6192. DOI: 10.7717/peerj.6192

Moudrý V., Devillers R. 2020. Quality and usability challenges of global marine biodiversity databases: An example for marine mammal data. *Ecological Informatics* 56: 101051. DOI: 10.1016/j.ecoinf.2020.101051

Namkhan M., Sukumal N., Savini T. 2022. Impact of climate change on Southeast Asian natural habitats, with focus on protected areas. *Global Ecology and Conservation* 39: e02293. DOI: 10.1016/j.gecco.2022.e02293

Newbold T. 2010. Applications and limitations of museum data for conservation and ecology, with particular attention to species distribution models. *Progress in Physical Geography* 34(1): 3–22. DOI: 10.1177/0309133309355630

Nunes L.A., Pearson R.G. 2017. A null biogeographical test for assessing ecological niche evolution. *Journal of Biogeography* 44(6): 1331–1343. DOI: 10.1111/jbi.12910

Palacký University Olomouc. 2020. *Climatic Conditions of the Czech Republic*. Available from https://geography.upol.cz/soubory/lide/smolova/GCZ/GCZ_Klima.pdf

Phillips S.J., Dudík M. 2008. Modeling of species distributions with Maxent: New extensions and a comprehensive evaluation. *Ecography* 31(2): 161–175. DOI: 10.1111/j.0906-7590.2008.5203.x

Phillips S.J., Anderson R.P., Schapire R.E. 2006. Maximum entropy modeling of species geographic distribution. *Ecological Modelling* 190(3–4): 231–259. DOI: 10.1016/j.ecolmodel.2005.03.026

Pillon Y., Chase M. 2007. Taxonomic exaggeration and its effects on orchid conservation. *Conservation Biology* 21(1): 263–265. DOI: 10.1111/j.1523-1739.2006.00573.x

R Core Team. 2023. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available from https://www.r-project.org/

Román-Palacios C., Wiens J.J. 2020. Recent responses to climate change reveal the drivers of species extinction and survival. *Proceedings of the National Academy of Sciences of the United States of America* 117(8): 4211–4217. DOI: 10.1073/pnas.1913007117

Salvà-Catarineu M., Romo A., Mazur M., Zielińska M., Minissale P., Dönmez A.A., Boratyńska K., Boratyński A. 2021. Past, present, and future geographic range of the relict Mediterranean and Macaronesian *Juniperus phoenicea* complex. *Ecology and Evolution* 11(10): 5075–5095. DOI: 10.1002/ece3.7395

Smith V.S., Blagoderov V. 2012. Bringing collections out of the dark. *ZooKeys* 209: 1–6. DOI: 10.3897/zookeys.209.3699

Soberón J., Peterson T. 2004. Biodiversity informatics: managing and applying primary biodiversity data. *Philosophical Transactions of the Royal Society B: Biological Sciences* 359(1444): 689–698. DOI: 10.1098/rstb.2003.1439

Sokal R.R., Rohlf F.J. 2012. *Biometry: The Principles and Practice of Statistics in biological Research*, *4th ed.* New York: W.H. Freeman and Company. 915 p.

Spooner F.E.B., Pearson R.G., Freeman R. 2018. Rapid warming is associated with population decline among terrestrial birds and mammals globally. *Global Change Biology* 24(10): 4521–4531. DOI: 10.1111/gcb.14361

Steffelová M., Traxmandlová I., Štípková Z., Kindlmann P. 2023. Pollination strategies of deceptive orchids – a review. *European Journal of Environmental Sciences* 13(2): 110–116. DOI: 10.14712/23361964.2023.12

Štípková Z., Kindlmann P. 2015. Extent and reasons for meadows in South Bohemia becoming unsuitable for orchids. *European Journal of Environmental Sciences* 5(2): 142–147. DOI: 10.14712/23361964.2015.87

Štípková Z., Kosánová K., Romportl D., Kindlmann P. 2018. Determinants of orchid occurrence: a Czech example. In: B. Şen, O. Grillo (Eds.): *Selected Studies in Biodiversity*. London: InTechOpen. P. 133–155. DOI: 10.5772/intechopen.74851

Štípková Z., Romportl D., Kindlmann P. 2020a. Which environmental factors drive distribution of orchids? A case study from South Bohemia, Czech Republic. In: J.M. Mérillon, H. Kodja (Eds.): *Orchids Phytochemistry, Biology and Horticulture*. Cham: Springer Nature. P. 1–33. DOI: 10.1007/978-3-030-38392-3_27

Štípková Z., Tsiftsis S., Kindlmann P. 2020b. Pollination mechanisms are driving orchid distribution in space. *Scientific Reports* 10(1): 850. DOI: 10.1038/s41598-020-57871-5

Švecová M., Štípková Z., Traxmandlová I., Kindlmann P. 2023. Difficulties in determining distribution of population sizes within different orchid metapopulations. *European Journal of Environmental Sciences* 13(2): 96–109. DOI: 10.14712/23361964.2023.11

Štípková Z., Tsiftsis S., Kindlmann P. 2021. Distribution of orchids with different rooting systems in the Czech Republic. *Plants* 10(4): 632. DOI: 10.3390/plants10040632

Swarts N.D., Dixon K.W. 2009. Terrestrial orchid conservation in the age of extinction. *Annals of Botany* 104(3): 543–556. DOI: 10.1093/aob/mcp025

Tsiftsis S., Djordjević V. 2020. Modelling sexually deceptive orchid species distributions under future climates: the importance of plant-pollinator interactions. *Scientific Reports* 10(1): 10623. DOI: 10.1038/s41598-020-67491-8

Warren D.L., Glor R.E., Turelli M. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution* 62(11): 2868–2883. DOI: 10.1111/j.1558-5646.2008.00482.x

Weterings R., Vetter K.C. 2018. Invasive house geckos (*Hemidactylus* spp.): their current, potential and future distribution. *Current Zoology* 64(5): 559–573. DOI: 10.1093/cz/zox052

Yi Y.J., Cheng X., Yang Z.F., Zhang S.H. 2016. Maxent modeling for predicting the potential distribution of endangered medicinal plant (*H. riparia* Lour) in Yunnan, China. *Ecological Engineering* 92: 260–269. DOI: 10.1016/j.ecoleng.2016.04.010

Zhang Z., Yan Y., Tian Y., Li J., He J.S., Tang Z. 2015. Distribution and conservation of orchid species richness in China. *Biological Conservation* 181: 64–72. DOI: 10.1016/j.biocon.2014.10.026

ПРИМЕНИМЫ ЛИ СВЕДЕНИЯ БАЗЫ GBIF В КАЧЕСТВЕ ИСХОДНЫХ ДАННЫХ ДЛЯ МОДЕЛИРОВАНИЯ ПРОСТРАНСТВЕННОГО РАСПРЕДЕЛЕНИЯ ВИДОВ? ИССЛЕДОВАНИЕ ИЗ ЧЕШСКОЙ РЕСПУБЛИКИ

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Вопросы, касающиеся изучения видового разнообразия, привлекают внимание экологов и биогеографов уже более столетия, главным образом потому, что разнообразие жизни на Земле быстро сокращается, что, как ожидается, продолжится и в будущем. На настоящий момент одной из наиболее крупных баз данных о распространении видов является Global Biodiversity Information Facility (GBIF), которая содержит более 2 миллиардов находок всех организмов, и это число постоянно увеличивается с добавлением новых данных и в сочетании с другими приложениями. Такие данные также содержатся в национальных базах данных, большинство из которых, к сожалению, часто не находятся в свободном доступе и не ассоциированы с GBIF. Мы предположили, что национальные базы данных, в основном профессионально поддерживаемые правительственными организациями, могут быть более полными, чем GBIF, который не имеет централизованной организации, и что поэтому национальные базы данных могут давать более точные прогнозы распределения видов, чем GBIF. Чтобы проверить наши гипотезы, мы сравнили: (1) объем данных, включенных в базу данных Чешской Республики «Nálezová databáze ochrany přírody» (NDOP, [База данных местонахождений для охраны природы]), с объемом данных в GBIF в пределах территории Чешской Республики, и (2) перекрытие прогностических карт пространственного распределения видов в Чешской Республике на основании этих двух баз данных. В качестве модельной группы растений мы использовали семейство Orchidaceae. Мы обнаружили, что: (i) существует значительно большее количество записей для территории исследования (Чешская Республика) в базе NDOP по сравнению с базой GBIF, и (ii) прогнозы пространственного распределения видов с использованием Maxent, основанные на информации о местонахождениях орхидей в базе NDOP, в значительной степени перекрываются с таковыми, основанными на данных о местонахождениях видов в базе GBIF. Учитывая эти результаты, мы полагаем, что, если для исследуемой территории доступна только одна база данных, необходимо использовать именно ее. Если же для территории исследования доступно больше баз данных, мы должны использовать ту из них, которая включает большее количество местонахождений видов (обычно это одна из баз данных местного значения, как NDOP), поскольку использование большего количества местонахождений подразумевает более высокую значимость моделирования пространственного распределения видов.

Ключевые слова: Global Biodiversity Information Facility, NDOP, базы данных, модели распределения видов, распространение орхидей

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ОРИГИНАЛЬНЫЕ СТАТЬИ

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Журнал «Nature Conservation Research. Заповедная наука» был учрежден в 2016 г. Его целью является освещение качества и уровня научных исследований, проводимых на территории заповедников и национальных парков всего мира, изучение их биологического разнообразия, а также биологии и экологии редких видов.

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Cover photo: Skua (*Stercorarius maccormicki*) in flight on the Haswell Archipelago, Davis Sea (Author: Dr. S.V. Golubev)

Фото на обложке: Южно-полярный поморник (*Stercorarius maccormicki*) в полете над архипелагом
Хасуэлл, море Дейвиса (Автор: к.б.н. С.В. Голубев)

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