1   ARTHROPOD BIOMASS INCREASE IN SPRING CORRELATES WITH NDVI IN

2   GRASSLAND HABITAT

3

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11

12   **ABSTRACT**

13   Data from remote sensing are often used as proxies to quantify biological processes, especially at

14   large geographical scales. The Normalized Difference Vegetation Index (NDVI) is the most

15   frequently used proxy for primary productivity. Assuming a direct, positive interrelation between

16   primary and secondary production in terrestrial habitats, NDVI is often used to predict food

17   availability for higher trophic levels. However, the relationship between NDVI and arthropod

18   biomass has rarely been tested. In this study, we analyzed extensive datasets of arthropod

19   communities from semi-natural grasslands in central Europe to test the relationship between

20   arthropod biomass of consumer trophic levels ('herbivores', 'mixed' and 'carnivores') in

21   grassland communities and NDVI during the spring season. We found that arthropod biomass

22   generally increased with NDVI. The same positive relationship between biomass and NDVI was

23   observed for each individual trophic level. Cross-correlation analyses did not show statistically

24   significant lags between the NDVI and biomass of herbivores and carnivores. All in all, our study

25   provides correlational evidence for the positive relation of primary and secondary productivity in

26   temperate terrestrial habitats during spring. Moreover, it supports the applicability of NDVI data

27   as a suitable habitat-specific proxy for the food availability of insectivores during spring.

28

29   Keywords: Primary productivity; Secondary productivity; Proxy; Food abundance;

30   Insects; Remote sensing.

31

INTRODUCTION

33   The availability of nutritional resources can critically influence community composition

34   and species richness (Mittelbach et al. 2001; Ribas et al. 2003). Animals in seasonal

35   habitats must deal with temporal variation in resource availabilities caused by periodic

36   changes in vegetation structure (Stinson and Brown 1983) and habitat quality (Wiegand

37   et al. 2008). However, estimating resource availability is often difficult to achieve,

38   especially when large and/or remote areas should be sampled. Thus, ecologists frequently

39   use proxies derived from remotely sensed data (Pettorelli et al. 2011; Stephens et al.

40   2015). Their application requires knowledge about the underlying relationship between

41   the measured and the predicted traits. Such interrelation is relatively easy to establish if

42   these traits are directly linked, as occurs between marine primary productivity and

43   phytoplankton abundance (Marshall and Nesius 1996) or primary productivity and plant

44   biomass in terrestrial ecosystems (Scurlock et al. 2002). However, approximations

45   encompassing multiple trophic levels are harder to evaluate.

46   In ecology, a frequently used indicator for resource approximations is the Normalized

47   Difference Vegetation Index (NDVI), a measure of primary productivity used for many

2

48 years in remote sensing. NDVI distinguishes the reflectance properties of the vegetation

49 (NIR-Red)/(NIR+Red), with NIR representing the near-infrared and Red the visible red

50 light reflected by the surface (Myneni et al. 1995). Nowadays, NDVI data are globally

51 available (e.g., www.star.nesdis.noaa.gov). The temporal and spatial resolution of these

52 data have improved over time and are, therefore, ideal for the analysis of vegetation

53 dynamics at large scales.

54 The applicability of NDVI for quantifying various habitat properties has been repeatedly

55 demonstrated. Thus, NDVI has been proven as a good proxy to estimate plant biomass

56 (Weiser et al. 1984), vegetation quality (Hamel et al. 2009), and crop yield (Fuller 1998).

57 Moreover, NDVI has been used to predict food availability for animals at higher trophic

58 levels such as raptors overwintering in the Sahelian zone feeding on grasshoppers

59 (Trierweiler et al. 2013) or kestrels at their breeding sites feeding on small mammals

60 (Smith et al. 2017). Various predators like insectivorous mammals and birds adjust their

61 annual cycles, especially the timing of breeding and migration (Perrins 1970; Jonzén et

62 al. 2007), to the abundances of terrestrial arthropods, which serve as their main food

63 source (Bell 1990; Morse 1971).

64 Several aspects concerning NDVI and arthropod biology have been revealed by previous

65 research. For instance, Lassau and Hochuli (2008) demonstrated that NDVI of the open

66 forest canopy is positively correlated with species richness and abundance of beetles in

67 Australian dry forests. Changes in NDVI of birch forest has been shown to correlate with

68 caterpillar abundance of geometrid moths in Fennoscandia (Jepsen et al. 2009); and NDVI

69 of shrubs has been found to correlate with locust abundance (Deveson 2013). It is also

70 known that the response of arthropod abundances to changes in NDVI can be delayed as

71 a result of developmental time from larva to imago or reproduction of the next generation

3

72 (Apiwathnasorn et al. 2006). Thus, the relation between NDVI and arthropods can differ

73 according to life-history traits of species.

74 Arthropod biomass is a good parameter to quantify resources available for consumers of

75 higher trophic levels. However, studies directly relating NDVI to arthropod biomass are

76 scarce (Sweet et al. 2015). Thus, ecologists urgently need empirical support for using

77 NDVI as a proxy for resource availability in insectivorous species.

78 Here, we related vegetation productivity derived from NDVI data to the biomass of

79 arthropods in semi-natural grasslands in central Europe. Specifically, we investigated if

80 and how the arthropod biomass of different trophic levels responds to the seasonal

81 increase in NDVI that occurs during spring. As the phenology of arthropods may vary

82 due to species-specific developmental times (Jarošík et al. 2011), we expect trophic levels

83 to differ in their response to changes in vegetation phenology, i. e. the existence of lags

84 between NDVI and biomass within the trophic levels.

85

86 **MATERIAL AND METHODS**

87 <u>Study area</u>

88 We studied the relationship between primary productivity and arthropod biomass in semi-

89 natural grassland (semi-dry meadows) at three sites (Gleitz, Johannisberg, and Leutratal)

90 in eastern Germany between 1987 and 1989 (Appendix A). The study sites (180-300 m

91 a.s.l.) were situated on hill sites in distances of about 30 km. The regional climate is

92 humid-continental with low annual precipitation (<600 mm p.a.), and late winter as the

93 driest period during the year. During the 1980s, the thermic vegetation period (i.e., air

94 temperatures above 5° C) averaged at about 230 days (Bundesamt für Naturschutz, 2014).

4

95

Arthropod data

97 Arthropods were collected using identical methods throughout all three study sites and

98 study periods within the framework of the grassland project run by the Institute of

99 Ecology, Friedrich-Schiller University Jena (Germany).

100 In each study site, the sampling was carried out in two locations all year round, every

101 year, using pitfall traps and sweep-nets for collecting ground and herb layer dwelling

102 arthropods, respectively (for details see: Perner 1997; Malt and Perner 2002; Perner and

103 Malt 2002). Within every location and every two weeks, ten pitfall traps were checked

104 and ten double swings of sweep-netting in each of ten points were sampled. Each of these

105 ten sampling points were randomly distributed coordinates around every location, in its

106 vicinity, and with similar characteristics. Pitfall traps operated continuously, and the

107 individuals trapped therein were collected the mid-day on the same day as sweep-netting

108 was carried out.

109 In most cases, arthropods were determined to species level and, in some cases, only to

110 family-level.

111

Trophic levels and biomass

113 We assigned each species to one of the following trophic levels: 'herbivores', 'mixed',

114 and 'carnivorous arthropods' based on information on main diet and foraging behavior

115 (Table 1). 'Mixed' category included omnivorous species and those that forage as

116 herbivorous or carnivores during different stages of their life cycle. If species' specific

117 information was not available (64% of cases), we categorized the species according to the

118 typical trophic level of its genus or family.

119 Table 1. Description of trophic levels for the arthropod species sampled, the number of
120 collected species, and the range of body mass across species (mg).

Trophic level	Number of species	
		Biomass (mg)
Herbivores	445	0.014 – 405.7
'Mixed'	189	0.028 – 338.6
Carnivores	305	0.039 – 278.8

121

122 To estimate the biomass per species, we multiplied species abundance (i.e., the total

123 number of individuals irrespectively of the life stage) with body mass according to the

124 following allometric relationship between body mass and body length: body mass (mg)

125 $= 0.0305 \times$ body length (mm) $^\wedge$ 2.62 (Rogers et al. 1976). Data on typical body length for

126 each species were obtained from Gossner et al. (2015). For the species not described in

127 Gossner et al. (2015) – 32% of the total –, body length information was obtained from

128 Watson and Dallwitz (2015) instead. Afterward, we summed biomasses of species within

129 the trophic levels, for each sampling date and site, irrespectively of the method of

130 collection. Finally, biomass data were log-transformed to achieve normal distribution (log

131 (n+1) to avoid negative values).

132

133 NDVI data

134 We acquired NDVI data from the weekly 16x16km-gridded global dataset NESDIS

135 STAR VHP 16 available by of the National Oceanic and Atmospheric Administration

136 (NOAA) (https://www.star.nesdis.noaa.gov/smcd/emb/vci/VH/vh_ftp.php) using the R

137 package rndvi from GitHub (https://github.com/tavimalara/rndvi). For each study site and

138 sampling date, we assigned the NDVI value for the grid cell that includes the study site

139 and corresponds to the closest date available in the NOAA dataset. Due to the close

140 proximity between the study sites Johannisberg and Leutratal, the NDVI grid for the two

141 sites was the same.

142 We only considered the main growing season of vegetation, i.e., dates between the

143 minimal and maximal values of NDVI for each year. Therefore, we excluded all NDVI

144 and arthropod data after the annual NDVI maximum. The median duration for this

145 interval was 12 weeks (25 – 75% percentiles: 11 – 14 weeks). For descriptive comparison

146 between years, we determined the spring green-up date and the speed of green-up (Fig.

147 1, Appendix E), which refers to the date for the maximum slope of NDVI rising in a

148 certain year. These measurements inform about early vs. late spring seasons, and the

149 speed of the primary productivity increase. Both measurements were calculated by fitting

150 a logistic curve to the NDVI rise in spring, determined by its observed min and max

151 values, for each site and year.

152 Figure 1. Boxplot comparison (middle line shows the median, rectangles show 25-75%

153 quantiles and bar limits the range) of the two main studied variables in three study sites

154 in Germany. (a) NDVI values at the study sites with different NDVI grid cells.(b)

155 Arthropod biomass (g/sampling day) of species considered within 'mixed' (including

156 omnivorous species and those that forage as herbivorous or carnivores during different

157 stages of their life cycle), 'herbivores' and 'carnivores' trophic levels collected at these

158 sites.

159

160 <u>Statistics</u>

161 Because arthropod biomass may respond with delay to changes in vegetation

162 (Apiwathnasorn et al. 2006), we checked for time lags between NDVI data and the

163 response in arthropod biomass using cross-correlation analysis of weekly mean NDVI

164 and mean biomass. Time lags were considered relevant if the cross-correlation coefficient

165 for each period was above a certain significance level. To improve the cross-correlation

166 analysis, possible temporal autocorrelation within each time series were removed by

167 using the package TSA (Chan and Ripley 2012).

168 We described the variability of NDVI and biomass data across sites, trophic levels, and

169 years using LOESS curves. Further, we tested for the effect of NDVI – the explanatory

170 variable – on arthropod biomass – the response variable – by applying a generalized linear

171 model using the function lm of the package stats (R-Core Team, 2018). We included

172 trophic level as an explanatory variable and its interaction with NDVI

173 (log(biomass)~NDVI+trophic level+NDVI*trophic level). Homoscedasticity and normal

174 distribution of residuals were visually checked in the diagnostic plots.

175 We estimated the model coefficients using the maximum likelihood approach. All

176 analyses were done in R (R-Core Team, 2018).

177

178 **RESULTS**

179 <u>Arthropod sampling</u>

180 Of the 939 identified species or taxonomic groups, Coleoptera accounted for 45.0% of

181 the species, followed by Diptera (26.5%), Arachnida (18.7%), Auchenorrhyncha (7.9%),

182 and Orthopteroidea (1.8%). Also, most of the collected individuals belonged to

183 Coleoptera (27.6%), followed by Arachnida (24.5%). Sweep-netting captured 1.2 times

184 more individuals and 1.4 times more biomass than pitfall trappings.

185 <u>Variability in NDVI and arthropod biomasses during spring</u>

186　NDVI values did not differ between years (F=1.96; d.f.=1,113; P=0.16). Moreover, speed

187　of spring green-up was similar across sites (F=0.30; d.f.=1,3; P=0.62) and years (F=0.69;

188　d.f.=1,3; P=0.46). We found marginally significant differences in arthropod biomass

189　between sites (F=2.45; d.f.=2,112; P=0.09). Arthropod biomass varied between years

190　(F=4.83; d.f.=1,113; P<0.05), being lower in later years (Appendix C). In contrast, trophic

191　levels did not differ in their mean biomasses (F=2.96; d.f.=2,167; P=0.054) (Appendix

192　D).

193

194　<u>NDVI- arthropod biomass relationship</u>

195　We found a significant positive relationship between NDVI and biomass of arthropods

196　(t=3.36, P<0.001) (Table2, Fig. 2).

197

198　Table 2. Model output for the generalized linear model (GLM) relating arthropod biomass

199　of the trophic levels ('mixed, 'carnivores' and 'herbivores') to NDVI, including its

200　interaction. 'Mixed' trophic level was used as reference level. The table shows the

201　estimates of the resulting coefficients, their standard errors (SE) and test statistics to

202　assess the rejection of the null hypothesis (under which these estimates are zero).

203　Measures of goodness of fit (D-squared proportion; null deviance and residual deviance)

204　of the models are included as footnotes.

Coefficients	Estimate	SE	t-value	Pr(>|t|)
Intercept	4.597	0.418	10.985	<0.001
NDVI	4.171	1.241	3.361	<0.001
trophic level				
herbivore	-2.860	0.599	-4.771	<0.001
carnivore	0.594	0.600	0.989	n.s.
NDVI*trophic level				

NDVI*herbivore	9.385	1.802	5.207	<0.001
NDVI*carnivore	0.474	1.770	0.268	n.s.

205   D-squared=0.478; Null deviance=395.86; Residual deviance=206.41

206

207   Figure 2. Relationship between arthropod biomass (g) (log-transformed) and NDVI.

208   Points show observed summed biomass (g) for each site, date, and trophic level;the black

209   line indicates the predicted relation obtained for the Generalized Linear Model

210   (log(biomass)~NDVI+trophic level+NDVI*trophic level), with 95% confidence intervals

211   shown in grey shade.

212

213   We derived similar results when each trophic level had been analyzed separately.

214   Herbivores' biomass was positively related to NDVI (t=10.49; P<0.001); carnivores'

215   biomass also showed a positive relationship to NDVI (t=5.34; P<0.001); and biomass of

216   'mixed' trophic level was positively related to NDVI as well (t=2.72; P<0.01).

217   Assumptions for linear modeling were visually checked, and its requirements fulfilled.

218   Cross-correlation analysis did not show statistically significant cross-correlation

219   coefficients for any lag considered between the NDVI and biomass of herbivores and

220   carnivores. The lack of a lag suggests that biomass is related to the NDVI value measured

221   most closely to the arthropod sampling date, as available in NOAA's weekly NDVI

222   dataset.

223

DISCUSSION

225   We found a direct, positive relationship between NDVI and arthropod biomass during the

226   main growing season (i.e., period from the minimal to the maximal NDVI value of each

227   year) in grassland habitats of eastern Germany. Thus, we provide (correlational) evidence

228 for the interaction between a primary production index and the concomitant change of

229 secondary production, which is frequently expected but has been rarely tested. The use of

230 NDVI as a proxy for arthropod biomass allows for temporal assessments of secondary

231 productivity in various fields, e.g., phenology of food availability for insectivorous

232 animals.

233 We are confident that our conclusions are robust because our study covers a significant

234 part of the local arthropod community, which had been collected in different vegetation

235 strata by different methods as well as across various sites and years. However, our

236 approach has some constraints which should be considered for generalization of the

237 findings.

238 Our study focused on the growing season starting in spring, i.e., the spring green-up when

239 seeds germinate, and new shoots and leaves grow (Cole et al. 2015), and when arthropods

240 become active, i.e., after hatch or cease of the winter dormancy period due to rising

241 ambient temperature (Jarošík et al. 2011). The beginning of the growing season offers

242 food with the highest protein contents and digestibility to herbivorous arthropods

243 (Crawley 1983; Mattson 1980), so it seems plausible that herbivores track this seasonal

244 food availability by increasing abundances (Kerby et al. 2012). More active and abundant

245 arthropods represent higher food availability for predators, which fine-tune the timing of

246 arrival on the breeding grounds (Jonzén et al. 2007) and the start of reproduction

247 according to spring phenology (Perrins 1970). Our study clearly indicates that NDVI is a

248 reasonable predictor for arthropod abundance in temperate grassland habitats during the

249 beginning of the growing season, and thus can be used as a proxy for food availability for

250 organisms at higher trophic levels, like e.g., migratory insectivorous birds at arrival or at

251 the beginning of their breeding (Newton 2004; Grande et al. 2009).

11

252　However, our short study period of a few subsequent years prevents further conclusions

253　regarding differences in maximum NDVI values between years and the related variation

254　in arthropod biomass. Our study system is situated in the temperate climate zone where

255　between-year variation in peak values is usually small and temporal shifts are more

256　prominent (early vs. late years; see also Appendix E for differences between years).

257　Moreover, NDVI data for our study period had a rather coarse resolution (16x16 km), and

258　thus a pixel representative for the study site also includes surrounding habitats, e.g.,

259　deciduous and coniferous forests, orchards, broad-leaved trees or other habitats

260　(Appendix B). Thus, the NDVI value represents a blend of habitat around the center of

261　the satellite grid cell. We believe that this limitation is not likely to affect the analysis of

262　temporal changes in NDVI, i.e., primary productivity in spring. Nevertheless, this

263　limitation might compromise further comparisons of NDVI between sites and habitats

264　during certain seasons, especially if surrounding habitats strongly differ between sites. If,

265　for instance, forests remain green and photosynthetically active, NDVI values generally

266　remain constant, while herbaceous vegetation might be already dried out, lowering the

267　NDVI value of that cell. Moreover, annual maximum NDVI values of a certain habitat

268　might not reflect maximum total primary productivity (Pinter et al. 1985, Wang et al.

269　2005) as various strata can differ in their seasonal pattern productivity, and certain groups

270　of arthropods may still respond specifically to strata-specific variation.

271

272　In this study, we assumed that arthropods respond similarly to environmental conditions

273　in spring. Moreover, we accounted for the vast variation in numbers of individuals and

274　body masses of various species by categorizing distinct trophic levels. This procedure has

275　a drawback for the applicability of NDVI-arthropod biomass interaction: to predict

276　biomass quantities, researchers should account for differential trophic level abundances

277 of arthropods species. However, the segregation of trophic levels allowed for checking

278 for temporal lags in the interaction of biomass to NDVI rise. Such response lags are

279 common as arthropods needs a certain time to complete their development; for instance,

280 mosquitoes abundance rises one month after the first rainfall in the tropics

281 (Apiwathnasorn et al. 2006). For temperate grasslands, we found no lagged response

282 between rising NDVI and arthropod biomass of the two main trophic levels studied

283 ('carnivores and 'herbivores'). Therefore, arthropods at our study sites more probably

284 responded to NDVI value within the measurement time intervals of two weeks between

285 subsequent NDVI measures. Thus, we contend that by using NDVI to predict arthropod

286 biomass in temperate regions, developmental times must not be necessarily considered.

287 However, trophic levels should preferably be considered when quantifying biomass from

288 NDVI, as the shape of the positive relation between biomass and NDVI can vary for the

289 different levels.

290

291 Conclusions

292 The positive and direct relationship between primary production and arthropod biomass

293 confirmed by this study allows predictions of arthropod biomasses in spring to be made

294 from remote sensing data, at least for temperate herbaceous habitats. Such assessments

295 of secondary productivity can help to disentangle phenology and distribution patterns of

296 consumers, i.e., the timing and the choice of stopover sites for birds on migration (Buler

297 et al. 2007; Hutto 1985), the arrival and timing of breeding in insectivorous animals (Both

298 et al. 2009), or may assist pest control management in agriculture at the beginning of the

299 growing season (Bravo et al. 2003).

300 To generalize the relationship between NDVI and secondary productivity for various

301 habitats, years, and locations, it is necessary to use long-term data sets of arthropods and

302 detailed entomological descriptions. Additionally, the currently and freely available

303 remote sensing data with higher resolution (e.g., 10x10m resolution of Sentinel-2/ EU-

304 Copernicus-Project) will enable future studies on primary productivity and related

305 arthropod abundances across years, different management schemes, and on small scales.

306 Code availability: Code available on request from the authors

307 Authors' contributions: All authors contributed equally to this work, including the

308 conception, development, and writing of this manuscript.

309 Data availability: This study was a re-analysis of field data collected in the 1980s within

310 the grassland project of the former Scientific Department Ecology (Wissenschaftsbereich

311 Ökologie) at the Friedrich-Schiller-University Jena (former German Democratic

312 Republic).

313 Compliance with ethical standards: Within the temporal framework of the field work for

314 this study, arthropod sampling had no legal restrictions in its location (former German

315 Democratic Republic).

316 Conflict of interest: The authors declare that they have no conflict of interest.

317 Ethics approval: Not applicable.

318

319 **BIBLIOGRAPHY**

320 Apiwathnasorn C, Asavanich A, Komalamisra N, Samung Y, Prummongkol S,

321 Kanjanopas K (2006) The relationship between the abundance of *Mansonia* mosquitoes

14

322   inhabiting a peat swamp forest and remotely sensed data. SE Asian J Trop Med 37: 463–

323   467.

324   Bell GP (1990) Birds and mammals on an insect diet: a primer on diet composition

325   analysis in relation to ecological energetics. Stud. Avian Biol 13:416–422.

326   Both C, Van Asch M, Bijlsma RG, Van Den Burg AB, Visser ME (2009) Climate change

327   and unequal phenological changes across four trophic levels: Constraints or adaptations?

328   J Anim Ecol 78: 73–83.

329   Bravo C, Moshou D, West J, McCartney A, Ramon H (2003) Early disease detection in

330   wheat fields using spectral reflectance. Biosyst Eng 84:137–145.

331   Buler JJ, Moore FR, Woltmann S (2007) A multi-scale examination of stopover habitat

332   use by birds. Ecology 88:1789–1802.

333   Bundesamt   für   Naturschutz   (2014)   https://biologischevielfalt.bfn.de/nationale-

334   strategie/indikatoren-und-berichterstattung/indikatorenbericht-2014/indikatoren/dauer-

335   der-vegetationsperiode.html.

336   Chan KS, Ripley B (2012) TSA: Time series analysis. R package version, 1.

337   Cole EF, Long PR, Zelazowski P, Szulkin M, Sheldon BC (2015) Predicting bird

338   phenology from space: Satellite-derived vegetation green-up signal uncovers spatial

339   variation in phenological synchrony between birds and their environment. Ecol Evol

340   5:5057–5074.

341   Cover CL (2000) Corine Land Cover. European Environment Agency, Copenhagen.

342   Crawley MJ (1983) Herbivory. The dynamics of animal-plant interactions. Blackwell

343   Scientific Publications.

15

344 Deveson ED (2013) Satellite normalized difference vegetation index data used in

345 managing Australian plague locusts. J Appl Remote Sens 7:75–96.

346 Fuller DO (1998) Trends in NDVI time series and their relation to rangeland and crop

347 production in Senegal, 1987-1993. Int J Remote Sens 19:2013–2018.

348 Gossner MM, Simons NK, Achtziger R, Blick T, Dorow WH, Dziock F et al (2015) A

349 summary of eight traits of Coleoptera, Hemiptera, Orthoptera and Araneae, occurring in

350 grasslands in Germany. Sci Data 2:150013.

351 Grande JM, Serrano D, Tavecchia G, Carrete M, Ceballos O, Díaz-Delgado R, JL Tella,

352 Donázar J A (2009). Survival in a long-lived territorial migrant: effects of life-history

353 traits and ecological conditions in wintering and breeding areas. Oikos 118: 580–590.

354 Hamel S, Garel M, Festa-Bianchet M, Gaillard JM, Côté SD (2009) Spring Normalized

355 Difference Vegetation Index (NDVI) predicts annual variation in timing of peak faecal

356 crude protein in mountain ungulates. J Appl Ecol 46:582–589.

357 Hutto RL (1985) Seasonal changes in the habitat distribution of transient insectivorous

358 birds in southeastern Arizona: competition mediated? Auk 102:120–132.

359 Jarošík V, Honěk A, Magarey RD, Skuhrovec J (2011) Developmental Database for

360 Phenology Models: Related Insect and Mite Species have Similar Thermal Requirements.

361 J Econ Entomol 104:1870–1876.

362 Jepsen JU, Hagen SB, Høgda KA, Ims, RA, Karlsen SR, Tømmervik H, Yoccoz NG

363 (2009) Monitoring the spatio-temporal dynamics of geometrid moth outbreaks in birch

364 forest using MODIS-NDVI data. Remote Sens Environ 113:1939–1947.

365 Jonzén N, Hedenström A, Lundberg P (2007) Climate change and the optimal arrival of

366 migratory birds. Proc Biol Sci 274:269–74.

367 Kerby JT, Wilmers CC, Post E (2012) Climate change, phenology, and the nature of

368 consumer–resource interactions: advancing the match/mismatch hypothesis. Pages 508–

369 525 in Ohgushi T, Schmitz O, Holt RD, editors. (2012) Trait-mediated indirect

370 interactions: ecological and evolutionary perspectives. Cambridge University Press.

371 Lassau SA, Hochuli DF (2008) Testing predictions of beetle community patterns derived

372 empirically using remote sensing. Divers Distrib 14:138–147.

373 Malt S, Perner J (2002) Zur epigäischen Arthropodenfauna von landwirtschaftlichen

374 Nutzflächen der Unstrutaue im Thüringer Becken. Teil 1: Webspinnen und Weberknechte

375 (Arachnida: Araneae et Opiliones). Faun Abh Mus Tierkd Dresden 22: 207-228.

376 Marshall HG, Nesius KK (1996) Phytoplankton composition in relation to primary

377 production in Chesapeake Bay. Mar Biol 125: 611–617.

378 Mattson WJ (1980) Herbivory in Relation to Plant Nitrogen Content. Annu Rev Ecol Evol

379 S 11: 119–161.

380 Mittelbach GG, Steiner CF, Scheiner SM, Gross KL, Reynolds HL, Waide RB et al

381 (2001) What is the observed relationship between species richness and productivity?

382 Ecology 82:2381-2396.

383 Morse DH (1971) The Insectivorous Bird as an Adaptive Strategy. Annu Rev Ecol Evol

384 S 2:177–200.

385 Myneni RB, Hall FG, Sellers PJ, Marshak AL (1995) The interpretation of spectral

386 vegetation indexes. IEEE Geosci Remote Sens Lett 33:481–486.

387 Newton I (2004) Population limitation in migrants. Ibis 146: 197–226.

388 Perner J (1997) Zur Arthropodenfauna der Kalktrockenrasen im Mittleren Saaletal
389 (Ostthüringen). Teil 1: Coleoptera, Diptera, Auchenorrhyncha, Saltatoria, Araneae. Faun
390 Abh Mus Tierkd Dresden 21: 53-90.

391 Perner J, Malt S (2002) Zur epigäischen Arthropodenfauna von landwirtschaftlichen
392 Nutzflächen der Unstrutaue im Thüringer Becken. Teil 2: Käfer (Coleoptera). Faun Abh
393 Mus Tierkd Dresden 22:261 - 283.

394 Perrins CM (1970) The timing of birds' breeding seasons. Ibis 112:242–255.

395 Pettorelli N, Ryan S, Mueller T, Bunnefeld N, Jędrzejewska B, Lima M, Kausrud K
396 (2011) The Normalized Difference Vegetation Index (NDVI): Unforeseen successes in
397 animal ecology. Clim Res 46:5–27.

398 Pinter Jr PJ, Jackson RD, Elaine EC, Gausman HW (1985) Sun-angle and canopy-
399 architecture effects on the spectral reflectance of six wheat cultivars. Int J Remote Sens
400 6:1813–1825.

401 R-Core Team (2018) R: A language and environment for statistical computing. R
402 Foundation for Statistical Computing, Vienna, Austria.

403 Ribas CR, Schoereder JH, Pic M, Soares SM (2003) Tree heterogeneity, resource
404 availability, and larger scale processes regulating arboreal ant species richness. Austral
405 Ecol 28: 305-314.

406 Rogers LE, Hinds WT, Buschbom RL (1976) A general weight vs. length relationship for
407 insects. Ann Entomol Soc Am 69:387–389.

408 Scurlock JM, Johnson K, Olson RJ (2002) Estimating net primary productivity from

409 grassland biomass dynamics measurements. Glob Change Biol 8: 736–753.

410 Smith SH, Steenhof K, McClure CJ, Heath JA (2017) Earlier nesting by generalist

411 predatory bird is associated with human responses to climate change. J Anim Ecol 86:98–

412 107.

413 Stephens PA, Pettorelli N, Barlow J, Whittingham MJ, Cadotte MW (2015) Management

414 by proxy? The use of indices in applied ecology. J Appl Ecol 52:1–6.

415 Stinson CSA, Brown VK (1983) Seasonal changes in the architecture of natural plant

416 communities and its relevance to insect herbivores. Oecologia 56:67-69.

417 Sweet SK, Asmus A, Rich ME, Wingfield J, Gough L, Boelman NT (2015) NDVI as a

418 predictor of canopy arthropod biomass in the Alaskan arctic tundra. Ecol Appl 25:779–

419 790.

420 Trierweiler C, Mullie WC, Drent RH, Exo KM, Komdeur J, Bairlein F et al (2013) A

421 Palaearctic migratory raptor species tracks shifting prey availability within its wintering

422 range in the Sahel. J Anim Ecol 82:107–120.

423 Wang Q, Adiku S, Tenhunen J, Granier A (2005) On the relationship of NDVI with leaf

424 area index in a deciduous forest site. Remote Sens Env 94:244–255.

425 Watson L, Dallwitz M (2015) British insects. http://delta-intkey.com. Version: 25th

426 January 2015.

427 Weiser RL, Asrar G, Miller GP, Kanemasu ET (1984) Assessing Biophysical

428 Characteristics of Grassland from Spectral Measurements. Machine Processing of

429 Remotely Sensed Data Symposium 152: 141–152.

19

430 Wiegand T, Naves J, Garbulsky MF, Fernández N (2008) Animal Habitat Quality and

431 Ecosystem Functioning: Exploring Seasonal Patterns Using Ndvi. Ecol Monogr 78: 87–
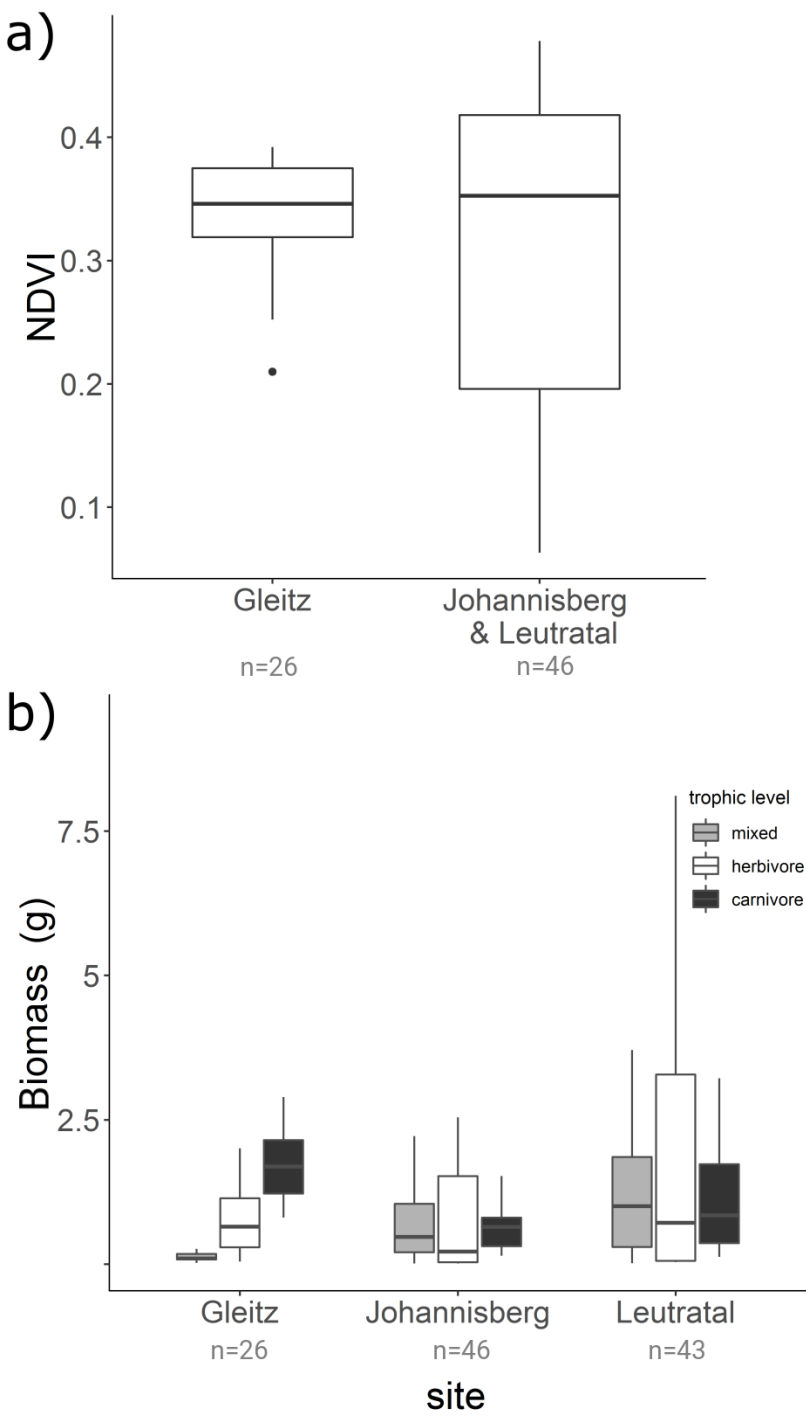
432 103.

Figure1

Figure2