



# Temporal homogenization of functional and beta diversity in bird communities of the Swiss Alps

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## Abstract

**Aim:** Describing the spatio-temporal dynamics of biotic communities is critical for understanding how environmental change can affect biodiversity. Mountains are especially susceptible to such changes (e.g., climate change) and, consequently, have been identified as ecosystems of conservation concern. With their sharp physical and ecological transitions, altitudinal gradients allow examining the influence of different climatic conditions and land use types on species assemblages across small spatial extents, and thus, they constitute natural laboratories to study diversity–environment relationships.

**Location:** Switzerland.

**Methods:** We take advantage of long-term (20 years) monitoring data and an extensive trait dataset (100 traits) to examine spatial patterns, temporal trends, and spatio-temporal dynamics in functional and beta diversity of bird communities in the Swiss Alps.

**Results:** Functional diversity indices showed a congruent pattern over time and across space; most indices decreased over the study period and were strongly correlated with altitude. In agreement with studies from the tropics, we found that communities in the lowlands were functionally over-dispersed, whereas communities at higher elevations were functionally clustered. High-altitude communities exhibited high functional originality, low levels of niche differentiation and a high turnover rate. Beta diversity declined over the study period.

**Conclusions:** Our findings suggest that pastoral abandonment does not result in an increase in avian functional diversity as most species colonizing woody-encroached grasslands are functionally redundant, whereas alpine meadows are inhabited by species exhibiting a high degree of habitat specialization and unique functional traits. Hence, the tree line constitutes a boundary between two well-differentiated functional groups: one representing a functional continuum from lowlands dominated by agricultural landscape to high-mountain forests, and the other one composed of alpine communities. Overall, this study reveals a process of biotic homogenization (i.e., increasing functional similarity) across the last two decades in the Swiss Alps, coinciding with the recently reported increases in the abundance of generalist species.

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## KEYWORDS

alpine communities, altitudinal gradient, functional traits, monitoring, Switzerland

## 1 | INTRODUCTION

Understanding how biodiversity is distributed across space is a fundamental challenge in ecology (Tilman, 1999). Along altitudinal gradients, climatic conditions and habitats often vary greatly over small spatial extents, which makes altitudinal gradients excellent laboratories to study the spatial patterns of species assemblages. These ecosystems are especially sensitive to climate change as it has been shown that mountains seem to be warming at a higher rate than other regions (Catalan, Ninot, & Aniz, 2017; Guisan et al., 2019). Many previous studies have examined the spatial pattern in species richness along altitudinal gradients and showed that animal diversity tends to decline with increasing elevation (e.g., McCain & Grytnes, 2010; Smith, 2015). Despite their high dispersal capacity in comparison with other taxa, birds are not an exception (e.g., Herzog, Kessler, & Bach, 2005; Nogués-Bravo, Araujo, Romdal, & Rahbek, 2008). Climate has been suggested as the main factor shaping bird assemblages along these gradients as abiotic factors such as temperature and—in a lesser extent—precipitation govern the energy use, performance, and ultimately the abundance and distribution of birds via direct physiological constraints (Laiolo, Pato, & Obeso, 2018; McCain, 2009; Peters et al., 2016). Recent studies, however, have suggested that resource availability can also play a paramount role in determining spatial richness patterns (Ferber, Schleuning, Hemp, Howell, & Böhning-Gaese, 2014; Hanz et al., 2019).

Examining the functional trait composition of species assemblages can help to better understand the mechanisms that generate and maintain the observed diversity patterns along altitudinal gradients (Dehling et al., 2014; McGill, Enquist, Weiher, & Westoby, 2006). Functional traits capture different aspects of species' resource use and ecological requirements, and thus, they are potentially useful in improving biodiversity predictions under environmental change (e.g., Villéger, Miranda, Hernández, & Moullot, 2010; Villéger, Novack-Gottshal, & Moullot, 2011). The small body of research on the subject has reported a decrease in functional diversity along altitudinal gradients at both local (e.g., Santillán et al., 2019) and continental (Morelli & Benedetti 2020) scales, suggesting that communities at high elevations are functionally more redundant and less prone to lose species with extreme traits.

A recurrent finding in the literature is the functional over-dispersion of species-rich communities in lowlands, a fact that has been attributed to higher interspecific competition, which limits the co-existence of functionally similar species (Dehling et al., 2014). Meanwhile, communities at higher elevations show functional clustering, likely due to environmental filtering as only species with specific traits will be able to persist under harsh conditions (e.g., Graham, Parra, Rahbek, & McGuire, 2009). Biotic interactions and environmental filters act therefore as selective agents on trait combinations and thus on functional diversity. The relative influence of

each of these processes is expected to vary along environmental gradients depending on latitude and biogeographic differences (Myers et al., 2013). It must be noted that, so far, most evidence comes from the tropics (mainly from the Ecuadorian Andes; Dehling et al., 2014; Hanz et al., 2019; Jankowski et al., 2013; Santillán et al., 2019), whereas there is a paucity of studies from the temperate region. A priori, the stronger seasonality and longer periods of snow cover and permafrost in temperate regions may result in sharper altitudinal gradients at mid latitudes because of the constraints imposed by a short growing season (Supriya, Moreau, Sam, & Price, 2019). Hence, elevation and latitude can interact to influence variation in avian functional traits, as it has been shown for life history traits (Balasubramaniam & Rotenberry, 2016). Consequently, some of the altitudinal patterns that have been consistently reported in tropical regions may not hold true in higher latitudes.

Volunteer-based bird monitoring programmes across Europe and North America allow the collection of massive abundance data across a wide range of environments. Although the main goal of such bird surveys is to quantify temporal trends in abundance and distribution in order to detect possible species declines, the obtained datasets provide an excellent opportunity to also study community dynamics over both space and time. Long-term data arising from standardized monitoring programmes constitute a valuable opportunity to determine temporal trends in species assemblages, but the number of studies making use of this resource is yet relatively small (Monnet et al., 2014; White, Montgomery, Storchová, Hořák, & Lennon, 2018).

Additional insight into the drivers shaping species assemblages might come from the comparison of the compositional similarities among species assemblages, also known as beta diversity,  $\beta$  (Whittaker, 1960). For instance, assessing changes in taxonomic assemblage composition along environmental gradients can guide strategies for protecting the biological diversity of a landscape (e.g., ranking priorities for conservation actions: Meynard et al., 2011, see also Jankowski, Ciecka, Meyer, & Rabenold, 2009). However, little is known about the patterns and causes of spatial variation in community composition across elevations. To date, the few studies that have investigated altitudinal changes in beta diversity are limited by low replication—they are often restricted to one or a few transects—and/or are conducted at small spatial scales (Kraft et al., 2011). Even scarcer are the studies combining measures of alpha and beta diversity along altitudinal gradients, despite some studies have highlighted the benefit of considering both components jointly (Meynard et al., 2011).

Under ongoing global change, mountain regions constitute ecosystems of conservation concern. Global warming, coupled with other stressors (e.g., habitat loss), is likely to have a massive impact on species distributions, abundances and interactions in these ecosystems (Lehikoinen et al., 2019; Lehikoinen, Green, Husby,

Kålås, & Lindström, 2014; Scridel et al., 2018). In the Alps, an increase in the mean temperature of about 1.7°C was recorded for the 30-year period 1975–2004, almost twice as much as the average global temperature increase (Rebetez & Reinhard, 2008). In addition, the abandonment of traditional grazing practices has led to substantial changes in land uses resulting in an upward shift of the tree line (Gehrig-Fasel, Guisan, & Zimmermann, 2007) as well as shrub and forest expansion (Bebi et al., 2017; Gellrich, Baur, Koch, & Zimmermann, 2007; Laiolo, Dondero, Ciliento, & Rolando, 2004). Hence, rapid climate change and land abandonment may act in concert shaping species distribution and assemblage compositions in the region. There is evidence that the altitudinal distribution of some bird species in Switzerland has shifted upwards in the past two decades (Bani, Luppi, Rocchia, Dondina, & Orioli, 2019; Maggini et al., 2011; Pernollet, Korner-Nievergelt, & Jenni, 2015; Vittoz et al., 2013). However, how these patterns translate into changes at the community level remains unknown. Assessing how diversity and community structure of primary consumers are influenced by environmental gradients through bottom-up effects is paramount to better understanding and predicting future changes in ecosystem functioning and dynamics in high-altitude landscapes. Here, we used long-term monitoring data on bird species abundance and an extensive trait dataset to examine spatial patterns and temporal trends in functional and beta diversity of land bird communities in the Swiss Alps. We predict the following: (a) lower functional diversity and higher trait convergence in high-altitude communities as result of environmental filtering (e.g., Dehling et al., 2014), and, (b) an overall decrease in functional and beta diversity in congruence with the increase of generalist species observed at a population level (Knaus et al., 2018).

## 2 | MATERIAL AND METHODS

### 2.1 | Bird data

We used data from the Swiss breeding bird monitoring scheme (“Monitoring Häufige Brutvögel” MHB) collected from 1999 to 2018. This programme consists of 267 1 × 1 km cells that are laid out as a grid across Switzerland, of which 157 are located in the Alps. Each one of these sites is monitored yearly by skilled volunteer ornithologists following a standardized territory mapping protocol (Kéry & Schmid, 2006). Observers record every bird detected by visual or acoustic contact along a transect route that did not change over the years. Surveys were conducted three times (twice above the timberline) during the breeding season. Observers then delineate territories for all species, which subsequently are summed to the total number of territories per km<sup>2</sup> and year.

Our sample consisted of 151 out of 157 plots distributed across the Swiss Alps; six had high percentages of urban land use and were not considered. Raptors like eagles and hawks were excluded from analyses as the point count method is not suited to their large home ranges. Likewise, species that only breed in wetlands (e.g., egrets,

crakes, rails) were not included as they were not properly monitored by this methodology. To diminish the effect of rare species (i.e., those species whose records are only anecdotal), we selected species that were recorded in at least 100 sampling plots over the study period and at least once every year. We considered a total of 97 species, which account for 99% of the total number of counted territories.

### 2.2 | Environmental variables

We considered five environmental variables, three continuous (altitude, climatic conditions and habitat heterogeneity) and two categorical (habitat and subregion), in our analyses. To assess among-plot climatic variability, we extracted 19 bioclimatic variables (*bio1-bio19*) for each plot (2.5-arc-minute resolution) from the WORLDCLIM database ([www.worldclim.org](http://www.worldclim.org); Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). As many of them are strongly correlated with each other, to avoid multicollinearity, we performed a principal component analysis, which yielded a first factor (PC1) accounting for 75% of the total variance. PC1 correlated positively with mean annual temperature ( $R^2 = .88$ ;  $p < .001$ ) and negatively with annual precipitation ( $R^2 = .85$ ;  $p < .001$ ). We used the inverse Simpson's diversity index to obtain a quantitative estimate of the level of habitat heterogeneity in each plot from a matrix including the percentage of land use corresponding to 24 different categories. Land use information (geostat data at 1 × 1 km<sup>2</sup> resolution) was obtained from aerial surveys carried out by the Swiss Federal Office for Statistics ([www.bfs.admin.ch](http://www.bfs.admin.ch)). Study plots were classified into five biogeographic subregions (Northern, Southern, Eastern, Western and Pre-Alps) following the classification established in Gonseth, Wohlgemuth, Sansonnens, and Buttler (2001) and five dominant habitat types (farmland, forest, mixed and alpine).

### 2.3 | Functional traits

We compiled a matrix of 100 traits for the 97 species including morphological traits (body mass, brain mass), life history traits (fecundity, life span), traits linked to habitat use or feeding diet (e.g., foraging method, proportion of seeds in diet) and ecological traits (e.g., nest location, migratory behaviour). Traits were compiled from the literature and published databases (Myhrvold et al., 2015; Pearman et al., 2014; Tsuboi et al., 2018; Wilman et al., 2014). Then, we computed a matrix of functional distances between all pairs of species using Gower's distance, because we had both ordinal and nominal traits. Functional distances were calculated using the “*dist.ktab*” function in *ade4* (Dray & Dufour, 2007) after grouping all traits into eight different blocks and ensuring they had similar weights (Table S1). From this matrix of functional distances, we carried out a principal coordinates analysis and the resulting first seven axes were used as input to calculate the indices of functional diversity (next section). The functional space defined by these seven dimensions provides an accurate representation of the functional dissimilarity

between species (Mantel's test between Gower's distance on trait values and Euclidean distance in the seven-dimensional convex hull:  $p < .001$ ).

## 2.4 | Quantifying functional diversity

We calculated four multivariate indices of functional diversity for each of the 2,995 bird communities: functional richness, functional divergence, functional evenness and functional originality. Functional richness (FRic) is the volume of the synthetic niche space encompassed by the outermost vertices of the assemblage (i.e., convex hull volume). Functional divergence (FDiv) quantifies the proportion of biomass on the periphery of the niche space representing species with extreme trait combinations, based on the average distance from the centroid of the assemblage. Functional evenness (FEve) measures whether mean species traits are regularly distributed within the trait space indicating the existence of under- or overutilization of resources. Functional originality (FOri) (also called functional uniqueness) represents the average pairwise distance between a species and its nearest neighbour in niche space. FRic is naturally positively correlated with species richness—the more species there are, the larger the functional space occupied—whereas FDiv is partially influenced by species richness (SR). Consequently, to control for underlying variation in SR among plots, we also calculated standardized effect sizes of FRic and FDiv ( $SES_{FRIC}$  and  $SES_{FDiv}$ , respectively) for each community using null models generated by reshuffling community data matrix while maintaining occurrence frequency and species richness (“independent-swap” algorithm, 999 iterations). Standardized effect size (SES) is computed as  $(obs - \text{mean}(rand))/sd(rand)$ , *obs* being the observed value and *rand* the randomized value. A positive SES indicates a higher value of the index than expected by chance given the number of species, while a negative SES indicates a lower value. FEve and FOri are independent of SR; thus, these indices were not standardized. Functional diversity indices were calculated using the function “multidimFD” written by Sebastien Villéger (Villéger, in preparation).

We tested for the effect of altitude and remaining environmental variables on the different functional diversity metrics using generalized linear mixed models (GLMMs). Mean altitude, degree of habitat heterogeneity, climate (PC1) and study year were included as continuous covariates, whereas habitat type and subregion were included as categorical covariates. Study plot was fixed as random effect to avoid pseudoreplication. Initially, each GLMM was built with all explanatory terms fitted, including quadratic and cubic effects to account for potential nonlinear relationships. Final models were selected following a backward stepwise procedure, by progressively eliminating non-significant variables. The significance of the remaining variables was tested again until no additional variable reached significance. The result is the most parsimonious model for explaining the variation in the response variable, where only the significant explanatory variables are retained. Preliminary analyses using the

Moran's *I* autocorrelation index showed that there is no spatial autocorrelation in any response variable (all *p*-values > .25).

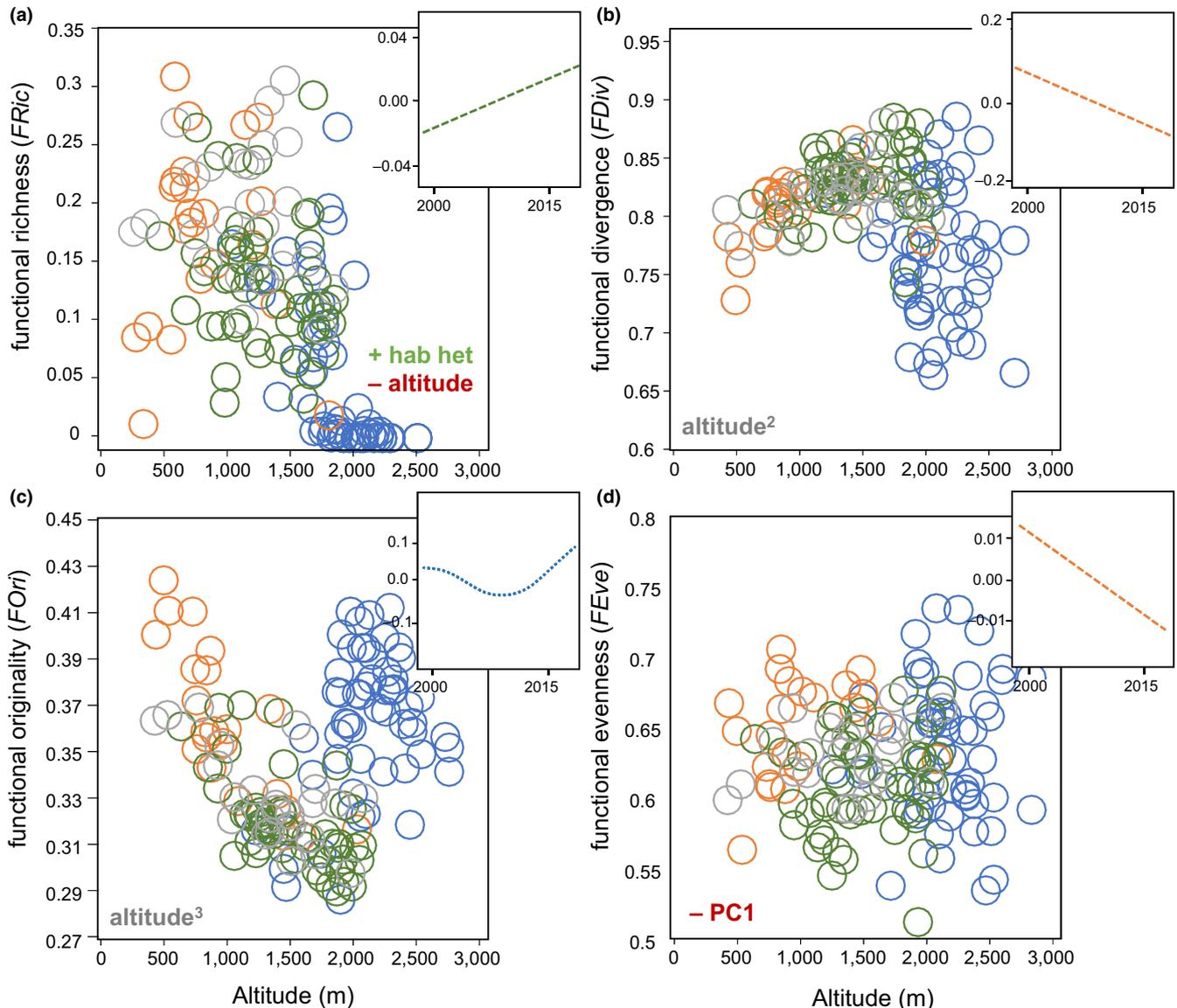
Next, we modelled functional diversity trends over 1999–2018 in search of possible nonlinearities or breakpoints in different functional indices using generalized additive mixed models (GAMMs; Wood, 2006). Mean altitude, habitat heterogeneity, PC1 and species richness (only for models with FRic or FDiv as response variable) were initially included as spline covariates. Habitat and subregion were included as explanatory factors. Plot identity was considered as a random effect to account for interannual variability. Plot coordinates were included as smoothed interaction term to account for spatial autocorrelation (e.g., Monnet et al., 2014). All response variables (i.e. functional diversity indices) were scaled to null mean and unit standard deviation (z-scores) prior to modelling in order to facilitate direct comparisons. Model fitting and analyses were conducted using the *mgcv* (Wood, 2011) and *itsadug* (van Rij, Wieling, Baayen, & van Rijn, 2017) packages.

In order to examine spatio-temporal trends in functional diversity, we constructed linear regression models for each time series in each survey plot (grid cell) using year as a continuous predictor. We then tested if the year slope, indicating the direction of temporal change in functional diversity, was related to altitude of the respective grid cell.

## 2.5 | Beta diversity

We tested for changes in community composition ( $\beta$  diversity) across space using pairwise dissimilarity matrices. First, we computed the Sørensen dissimilarity index ( $\beta_{sor}$ ), which accounts for the total compositional variation between assemblages. Second, we decomposed overall beta diversity into its turnover ( $\beta_{sim}$ ; Simpson's dissimilarity) and nestedness ( $\beta_{sne}$ ) components following the partitioning method of Baselga (2010). The turnover component captures compositional changes due to species replacement and is not affected by differences in taxonomic richness among sampling plots. The difference between  $\beta_{sor}$  and  $\beta_{sim}$  represents the nestedness component, whose value represents the extent to which poorer assemblages constitute subsets of richer assemblages. Nestedness of species assemblages, thus, reflects a deterministic process of species loss driven by any factor that promotes the non-random disaggregation of assemblages (Baselga, 2010).

Thereby, we obtained three distance matrices of pairwise dissimilarities ( $\beta_{sor}$ ,  $\beta_{sim}$  and  $\beta_{sne}$ ) for each study year, from which we computed three final matrices by averaging values obtained over the study period. Each one of these three matrices ( $\Delta y$ )—which constitutes robust estimates of the spatial variation in species composition across the study area—was then correlated with a matrix of geographic distances between plots using Mantel tests (1,000 permutations) in the R package *vegan* (Oksanen et al., 2013). We repeated this for three additional matrices of environmental distance, namely pairwise differences in altitude, climatic conditions and habitat type ( $\Delta x$ ). Although altitude and both temperature and precipitation (here summarized together with other climatic variables into a single principal component, PC1) are correlated, they do not bear



**FIGURE 1** Plots showing the relationship between different functional diversity indices (a: functional richness; b: functional divergence; c: functional originality; d: functional evenness) of land bird communities and altitude in the Swiss Alps. Each data point represents the mean value (averaged over the study period) for each community. Colours indicate the habitat type (orange: farmland; green: forest; grey: mixed; blue: alpine) to which each community belongs to. The insets show the temporal trend for each index (lines or smoothed curves fitted with generalized additive models) computed over the study period, 1999–2018. [Correction statement added on 06 June 2020 after first online publication: In figure 1, the title of x-axis (“Altitude (m)”) was inadvertently omitted and commas were wrongly added in the insets, the temporal variation (years) should read as “2000” and “2015” instead of “2,000” and “2,015”. These errors have been corrected in this version]

the same information. Altitude contains information on availability and seasonality of food resources, which constitute important constraints for birds especially during the breeding season. Meanwhile, climatic variables have a direct influence on birds' physiology. To keep both levels of information and disentangle the relative influence of altitude versus climatic conditions on community composition, we performed partial Mantel tests. This way, we explored the relationship between pairwise dissimilarities in community composition and pairwise differences in environment ( $\Delta y \sim \Delta x$ ; T3 in Anderson et al., 2011) in order to determine whether, for example, differences in bird community structure are related to differences in climatic conditions.

Complementarily, we fitted linear models including mean values of  $\beta_{\text{sor}}$ ,  $\beta_{\text{sim}}$  and  $\beta_{\text{sne}}$  computed for each plot (i.e., the mean of all pairwise

dissimilarities) as the dependent variables and altitude, degree of habitat heterogeneity, and PC1 as explanatory variables to test whether, for example, the turnover in community structure changed along an altitude gradient ( $\Delta y \sim x$ ; T2 in Anderson et al., 2011). In addition, to remove the influence of temperature and precipitation from altitude effects, we used the residuals of the regression between altitude and PC1 as a predictor (de Bello et al., 2013). In those cases in which the relationship was not linear, we built models including a quadratic term and tested for nonlinearity. Lastly, we assessed temporal changes in spatial  $\beta$ -diversity using GAMMs in a similar way to that previously described. Mean altitude, habitat heterogeneity and PC1 were included as spline covariates. Habitat and subregion were included as explanatory factors, whereas plot identity was included as random effect. We

also tested for spatio-temporal trends in  $\beta$ -diversity by examining the relationship between the slopes of year and altitude.

To avoid undefined values in dissimilarities caused by null denominators, we only considered those plots that were surveyed over the entire study period ( $n = 131$  plots). Beta-diversity estimates were computed using the *betapart* package (Baselga & Orme, 2012). All analyses were conducted in R version 3.5.2 ([www.r-project.org](http://www.r-project.org)).

### 3 | RESULTS

Species richness increased up to 1,000 m and then decreased with altitude, showing a low plateau-midpeak (LPMP) pattern (*sensu* McCain & Grytnes, 2010) (Figure S1). The average number of species per plot ranged from 6 to 48 (values averaged over 20 years; mean  $\pm$  SD =  $29.2 \pm 11.2$  species), being alpine environments and farmlands the habitats with lowest and highest taxonomic diversity, respectively (alpine:  $18.6 \pm 10.5$ ; forest:  $33.5 \pm 4.7$ ; mixed:  $37.6 \pm 4.5$ ; farmland:  $37.7 \pm 7.6$ ).

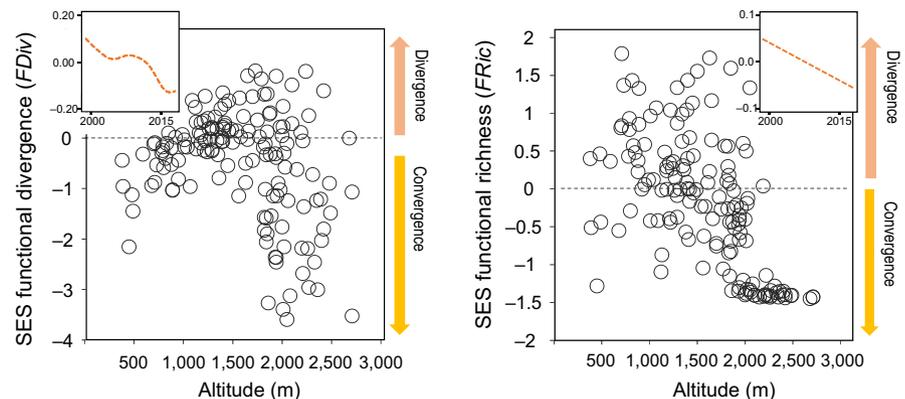
#### 3.1 | Functional diversity

All functional diversity indices varied among habitat types (all  $p$ -values  $< .001$ ; Table S2), whereas only functional richness (FRic) and its standardized effect size ( $SES_{FRic}$ ) varied significantly among subregions due to the lower values found in the Southern Alps and pre-Alps, respectively (Table S2). FRic increased with

habitat heterogeneity (hab het) and decreased with altitude (hab het:  $t = 7.33$ ,  $p < .001$ ; altitude:  $t = -4.43$ ,  $p < .001$ ; adj.  $R^2 = .63$ ; Figure 1). As the average number of species increased throughout the study period, FRic also showed a positive trend over time (Figure 1; Table S3). Functional evenness (FEve) did not correlate significantly with altitude, but with climatic conditions (PC1:  $t = -2.23$ ,  $p = .026$ ; adj.  $R^2 = .12$ ) and decreased over the study period (Figure 1; Table S3). Functional divergence (FDiv) correlated quadratically with altitude (altitude:  $t = 3.51$ ,  $p < .001$ , altitude<sup>2</sup>:  $t = -3.49$ ,  $p < .001$ ; adj.  $R^2 = .32$ ); it increased from 500 to 1,700 m and declined steeply above the tree line (from 1,700 to 2,000 m onwards). FDiv also showed a negative trend over time (Figure 1; Table S3). Functional originality (FOri) showed a cubic relationship with altitude (altitude:  $t = -4.97$ ,  $p < .001$ , altitude<sup>2</sup>:  $t = 3.95$ ,  $p < .001$ ; altitude<sup>3</sup>:  $t = -3.19$ ,  $p < .01$ ; adj.  $R^2 = 0.52$ ); it decreased from 500 m to 2,000 m and declined again from 2,000 m. No clear pattern emerged with respect to its temporal trend (Figure 1; Table S3). When considering “pure” estimators of functional richness and trait dispersion ( $SES_{FRic}$  and  $SES_{FDiv}$ ), at low and high altitude,  $SES_{FDiv}$  values were lower than those expected at random, indicating trait convergence, whereas at mid-altitude, values tended to be positive suggesting trait divergence (Figure 2).  $SES_{FRic}$  values only showed a clear trend from 2,000 m, wherein all sites displayed values of functional richness that were smaller than expected at random (Figure 2).

There was no significant relationship between the year and altitude slopes of the regression models fitted to each plot for any of the functional diversity metrics (all  $p$ -values  $> .1$ ).

**FIGURE 2** Variation of the standardized effect sizes (SES) of functional divergence (FDiv) and functional richness (FRic) across the altitudinal gradient. Values above (below) the dotted line indicate communities with FDiv or FRic or higher (smaller) than expected at random. The insets show the temporal trend for each index



**TABLE 1** Beta-diversity partitioning: results of full and partial Mantel tests correlating pairwise dissimilarity of bird land communities in the Swiss Alps (values averaged over a 19-year period) with pairwise distance or differences in environmental variables

Dissimilarity measure	Geographic distance	Altitudinal distance	Altitudinal (climatic)	Climatic distance	Climatic (altitudinal)	Habitat distance
Beta diversity ( $\beta_{sor}$ )	0.027	0.630*	0.572*	0.321*	-0.008	0.009
Turnover ( $\beta_{sim}$ )	0.038	0.702*	0.640*	0.377*	0.020	0.014
Nestedness ( $\beta_{sne}$ )	-0.018	-0.002	0.025	-0.047	-0.055 (0.062)	-0.012

Note: Partial Mantel tests are indicated with the control variable in parentheses (altitudinal (climatic) = the effects of altitudinal distance on community dissimilarity while controlling for climatic distance; climatic (altitudinal) = the effects of climatic distance on community dissimilarity while controlling for altitudinal distance). Asterisks denote  $p$ -values  $< .05$ .

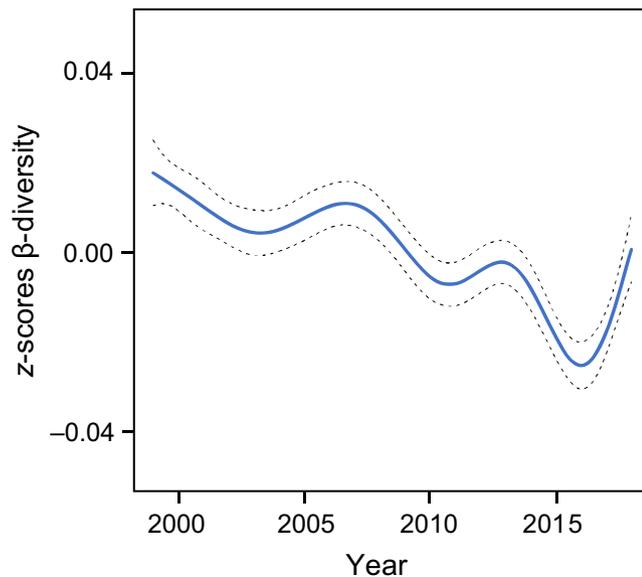
	Habitat heterogeneity	Altitude	Altitude residuals	Climatic index (PC1)
Beta diversity ( $\beta_{sor}$ )	$t = -6.10$ $p < .001$ $R^2 = .22$	$t = -10.71$ $p < .001$ $t' = 13.26$ $p' < .001$ $R^2 = .70$	$t = 5.25$ $p < .001$ $R^2 = .17$	$t = -0.97$ $p = .33$ $t' = 4.16$ $p' < .001$ $R^2 = .23$
Turnover ( $\beta_{sim}$ )	$t = -6.36$ $p < .001$ $R^2 = .23$	$t = -12.22$ $p < .001$ $t' = 14.06$ $p' < .001$ $R^2 = .66$	$t = 4.12$ $p < .001$ $R^2 = .11$	$t = 0.80$ $p = .42$ $t' = 4.72$ $p' < .001$ $R^2 = .18$
Nestedness ( $\beta_{sne}$ )	$t = -3.06$ $p < .01$ $R^2 = .06$	$t = 11.77$ $p < .001$ $R^2 = .51$	$t = 5.77$ $p < .001$ $R^2 = .20$	$t = -7.67$ $p < .001$ $R^2 = .31$
$\beta_{sne}/\beta_{sor}$ ratio	$t = 1.40$ $p = .16$	$t = 6.02$ $p < .001$ $t' = -4.70$ $p' < .001$ $R^2 = .35$	$t = 2.97$ $p < .01$ $R^2 = .06$	$t = -6.07$ $p < .001$ $t' = -2.51$ $p' < .05$ $R^2 = .23$

**TABLE 2** Results of modelling differences in  $\beta$ -diversity (and its two additive components, nestedness and turnover) versus environmental variables (habitat heterogeneity, altitude, altitude after correcting for climate, and climatic conditions)

### 3.2 | Beta diversity

The dissimilarity in species composition among sampling plots was positively correlated with both the difference in altitude and the degree of similarity in terms of climatic conditions among plots ( $\Delta y \sim \Delta x$  approach; Table 1). Partial Mantel tests showed that the correlation with altitude remained almost unchanged when controlling for climatic conditions. When controlling for altitudinal differences, however, the correlation between dissimilarity and climatic conditions became statistically non-significant, suggesting that this trend was

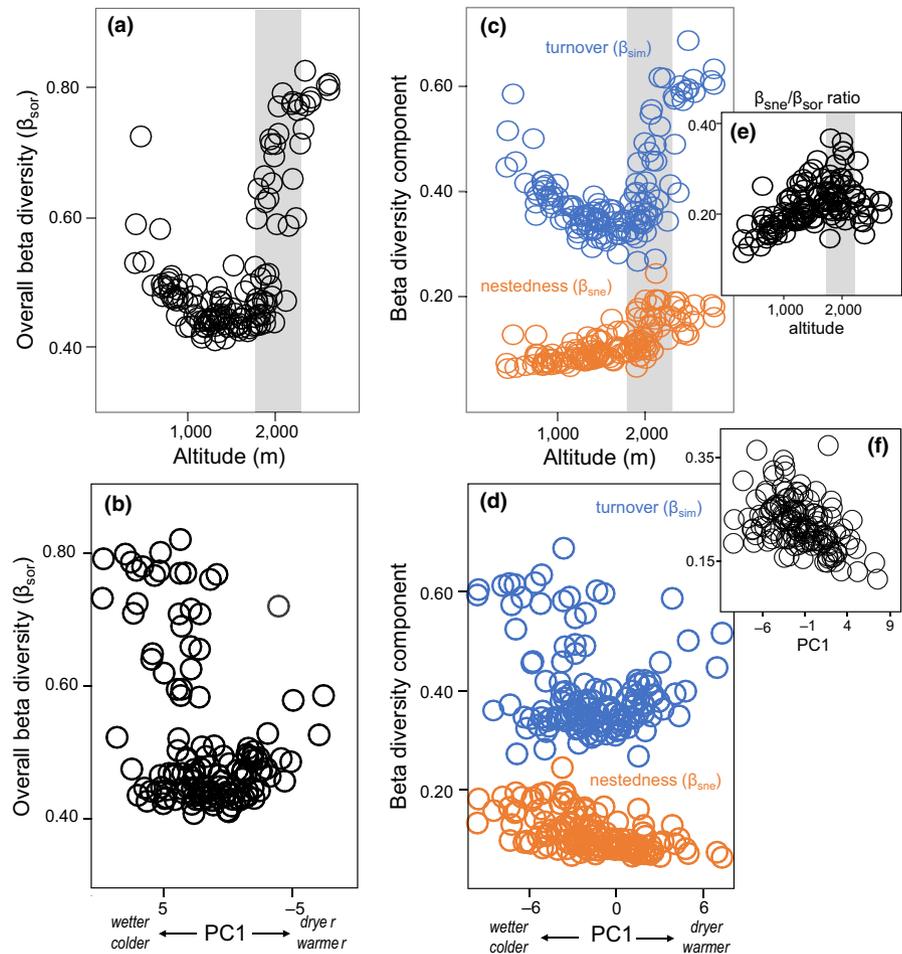
an indirect result of the altitudinal relationship (Table 1). The same pattern held true for the turnover component (species replacement), whereas for the nestedness component (species loss), the relationship became stronger when controlling for altitude (Table 1). Thus, the frequency with which species tended to replace each other increased as differences in altitude became greater regardless of the prevailing climatic conditions, while the relationship between the nestedness component and the level of climatic similarity indicated that assemblages located in more extreme environments tended to contain a subset of the species found in localities with more widespread climates (Table 1).



**FIGURE 3** Temporal variation of land birds' beta diversity in the Swiss Alps over the period 1999–2018. Beta-diversity values were computed using the Sørensen multiple site dissimilarity index and scaled to null mean and unit standard deviation to facilitate comparisons across years

Table 2 summarizes the results of modelling differences in  $\beta$  diversity versus environmental variables ( $\Delta y \sim x$  approach). Overall beta diversity ( $\beta_{sor}$ ) decreased from 380 to 1,800 m and increased sharply up to 2,700 m (Figure 3a). A similar U-shaped pattern was observed when plotting  $\beta_{sor}$  on the climatic axis, PC1 (Figure 3b). The nestedness component ( $\beta_{sne}$ ) was negatively and positively correlated with altitude and PC1, respectively, indicating that species loss is higher at higher altitudes (Figure 3c) and at warmer and dryer environments (Figure 3d). Meanwhile, the turnover component ( $\beta_{sim}$ ) showed patterns in relation to altitude and climatic conditions that resembled those described for  $\beta_{sor}$  (Figure 3c,d), as this component accounted for most (77%) of the variation in overall species  $\beta$  diversity. The relative influence of the nestedness versus turnover component correlated positively with altitude up to 1,800–2,000 m (Figure 3e) and negatively with PC1 (Figure 3f). From 2,000 m, the relative contribution of the nestedness component started to decrease, indicating that the high beta diversity observed at high altitudes was mainly due to a substantial increase of the rate of species replacement. When assessing the relationship between beta-diversity components and altitude without the pervasive effect of climatic conditions (i.e., altitude residuals), the linear negative relationship between  $\beta_{sne}$  and altitude remained invariant. Meanwhile, the slope of the negative

**FIGURE 4** Patterns of overall beta diversity ( $\beta_{sor}$ ), turnover ( $\beta_{sim}$ ), nestedness ( $\beta_{sne}$ ) and  $\beta_{sne}/\beta_{sor}$  ratio across the altitude and climatic gradient in the Swiss Alps. The shaded area indicates the altitudinal range of the tree line



relationship between  $\beta_{sim}$  and altitude observed at low and medium altitudes (<2,000 m) was much less steep (Figure S2). The relative contribution of the nestedness component ( $\beta_{sne}/\beta_{sor}$  ratio) increased along the gradient, but the downfall observed at high altitude was less marked than the observed one when using raw altitude values instead of residuals (Figure S2).

Beta diversity decreased during the study period (GAMM:  $F = 17.46$ , estimated degree of freedom  $edf = 7.96$ ,  $R^2 = .84$ ,  $p < .001$ ; Figure 4). There was no significant relationship between the slopes of the temporal trend and altitude ( $r = -.03$ ,  $p = .69$ ). The mean slope did not vary among habitat types ( $F_{3,127} = 0.44$ ,  $p = .72$ ) or subregions ( $F_{4,126} = 0.69$ ,  $p = .60$ ).

## 4 | DISCUSSION

In this study, we have examined spatio-temporal dynamics in functional and beta diversity of land bird communities over the last two decades in the Swiss Alps, a region that has been identified as particularly vulnerable to global change due to its complex topography and highly fragmented landscape. Both facets of biodiversity show a negative trend suggesting an impoverishment of communities from a functional and compositional perspective. Our work provides a comprehensive picture about how bird communities are responding to

human-induced changes in a mountain region, which is also exposed to rapid climatic changes. The study also highlights the negative effects that the upward shift of the tree line could have on mountain birds.

### 4.1 | Functional diversity

The observed nonlinear relationship between functional richness and altitude indicates that alpine communities are functionally clustered probably due to environmental filtering, which is strongest at extreme ends of gradients where only a small set of species with particular trait combinations are able to persist (Graham et al., 2009). This fact becomes even more evident when considering  $SES_{FRic}$ , whose values were consistently lower than expected at random. Highland communities also deviated from the pattern observed from low altitudes to 2,000 m in terms of functional divergence (FDiv). This index increased along the elevational gradient and decreased suddenly above the tree line indicating that the lack of tree cover drastically reduces the availability of niches. Because FDiv reflects the local equilibrium between the influences of biotic and abiotic factors, it seems that the strength of competition versus environmental filtering varies greatly with altitude. Such a result is not due to the existence of a lower taxonomic richness at high altitudes, as we found that  $SES_{FDiv}$  values were lower than expected by chance in accordance with that observed for FRic.

In terms of functional originality (FOri), the existence of two well-differentiated groups is clear, as illustrated in Figure 1 (see also Figure S3), one representing the transition from lowlands dominated by agricultural landscape to high-mountain forests (ranging from 500 to 2,000 m), and the other one strictly composed of alpine communities (>2,000 m). Thus, the tree line constitutes a break up between the farmland–forest continuum of species, in which birds associated with open habitats are progressively replaced by forest specialists, and the aggregate of species adapted to treeless vegetation environments. This indicates that gradual environmental change at lower altitudes may buffer functional composition until a tipping point is reached, where strong trait filtering may lead to a new functional composition. Thus, our results show that sudden changes in abiotic conditions at the tree line are reflected by trait discontinuities. In addition, the observed pattern suggests that species adapted to open habitats, either farmlands or alpine meadows, increase the level of FOri of communities.

Although we failed to find a significant relationship between functional evenness (FEve) and altitude, we observed a negative relationship between FEve and climatic conditions (PC1) suggesting an under-utilization of the niche space in colder and wetter environments. Interestingly, the absence of a clear trend for FEve values along the altitudinal gradient contrasts with results obtained by Morelli & Benedetti (2020), who reported a negative association between functional evenness of bird assemblages and elevation at a continental scale. It is worth mentioning that, according to their study, Switzerland is among the European regions whose avifauna exhibit a lower capacity (low resilience and functional evenness) to respond to strong ecological changes due to the country's intricate topography (Morelli & Benedetti 2020). However, the relationship between potential community resilience and elevation seems to be less obvious at a regional scale.

Functional diversity metrics exhibited a congruent pattern over time; most of them showed a negative trend during the 1999–2018 period. Particularly, notorious is the temporal decline in FEve indicating that bird communities are increasingly becoming less resilient and, thus, more vulnerable to the negative effects of natural or human disturbances. The lack of a significant relationship between the slope of the temporal regression models and altitude indicates that the observed decline is not specific to a particular elevational zone. It may be due to all environments in the Swiss Alps undergoing changes that impair functional diversity: agricultural intensification in the lowlands, the progressive decline of ancient forests and the expansion or cultivation or more homogeneous coniferous forests at mid-high elevations, and the abandonment of traditional agricultural practices in the mountains (Gellrich et al., 2007; Schifferli, Fuller, & Müller, 1999).

## 4.2 | Beta diversity

Mantel and partial Mantel tests showed that the frequency with which species tend to replace each other increased as differences

in altitude became greater regardless of the prevailing climatic conditions. Thus, although temperature constitutes an important abiotic filter along elevation gradients, with decreasing temperatures excluding successively more birds towards higher elevations, it seems that altitude per se represents a powerful structuring agent (Figure S2). This finding agrees with that reported by Hanz et al. (2019) in a recent study carried out in tropical mountains, wherein filtering of functional diversity was primarily driven by gradients in resource availability, whereas temperature and precipitation were less important factors. On the contrary, the nestedness component (non-random species loss) showed a tightest association with climatic distances indicating that the orderly disaggregation of assemblages is mainly promoted by differences in climatic conditions among sites.

Site-to-site variation in species composition ( $\beta$  diversity) decreased with increasing elevation up to 2,000 m. A similar distance decay, which describes the decrease in compositional similarity between two assemblages with increasing geographic distance/altitudinal difference, has been reported in previous studies (Soininen, Lennon, & Hillebrand, 2007). However, here, we found that  $\beta$ -diversity increased again above 2,000 m coinciding with a strong shift in vegetation structure. Thus, there is a gradual replacement of species along the elevational gradient followed by abrupt shift in species composition reflecting the singularity of high-mountain bird communities. Differences in  $\beta$ -diversity between local assemblages at mid- and high elevations probably reflect different mechanisms of community assembly (Sabatini, Jiménez-Alfaro, Burrascano, Lora, & Chytrý, 2018). For instance, the strength of dispersal limitation may predominate at higher altitudes, creating high dissimilarity among communities in the mountaintops.

When decomposing  $\beta$ -diversity ( $\beta_{sor}$ ) into its two components, we observed that the predominant component, turnover ( $\beta_{sim}$ ), showed a similar “hump-backed” pattern with altitude to that obtained for  $\beta_{sor}$ . Instead, the nestedness component ( $\beta_{sne}$ ) increases progressively up to 1,800–2,000 m suggesting a continuous impoverishment of species assemblages along the altitudinal gradient. That is, assemblages at medium–high altitudes constitute subsets of species assemblages located at low altitudes, while above the tree line bird communities are mainly composed by mountain specialists that cannot be found at lower altitudes.

In line with the observed temporal decrease in functional diversity, we detected a downward trend in  $\beta$  diversity suggesting a process of biotic homogenization, which is a cause of concern worldwide. The observed negative trend—which did not vary significantly across space—may be due to two non-mutually exclusive reasons: an overall loss of functionally rare species (subtractive homogenization) and functionally redundant (i.e., less original) species becoming more widespread (additive homogenization; Socolar, Gilroy, Kunin, & Edwards, 2016; see also Clavel, Julliard, & Devictor, 2010). The second alternative is more likely, given that generalist species are on the rise in Switzerland (Knaus et al., 2018) and other European countries (e.g., Clavero & Brotons, 2010; Devictor et al., 2008), which can

explain the existence of an increase in species richness over time. This result is in line with recent work showing that an increase in taxonomic diversity may be coupled with a functional homogenization of bird communities (Santillán et al., 2019).

### 4.3 | Conclusions

Our findings allow us to assert that pastoral abandonment does not result in an increase in avian functional diversity as most species colonizing woody-encroached grasslands are functionally redundant, whereas open habitats are inhabited by species exhibiting a high degree of habitat specialization and unique functional traits. In this context, the upper forest boundary plays a key role as it represents a functional barrier and a peak in species turnover. These results reinforce the idea that the upslope migration of the tree line ecotone constitutes one of the major threats for high-mountain bird communities (Chamberlain, Negro, Caprio, & Rolando, 2013; Ferrarini, Alatalo, & Gustin, 2017). Lastly, this study shows that the increase of generalist species detected at a population level in recent decades (Schmid, Kestenholtz, Knaus, Rey, & Sattler, 2018) translates into an overall loss of functional diversity and a decline in compositional (beta) diversity at community level, which is alarming and requires immediate conservation actions.

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### CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

### DATA AVAILABILITY STATEMENT

The data that support the findings of this study belong to the Swiss Ornithological Institute. Anyone interested in this dataset should contact this institution ([www.vogelwarte.ch](http://www.vogelwarte.ch)). The data are not publicly available due to ethical restrictions.

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#### BIOSKETCH

**Vicente García-Navas** is a research fellow at the University of Zurich, Switzerland. His current project is focused on diversity dynamics in land bird communities of the Swiss Alps. He is interested in how species assemblages change over time and along environmental gradients in a key region for studying resilience and vulnerability of communities and ecosystems in the face of global change.

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#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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