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Spatial heterogeneity in temporal dynamics of Alpine bird communities along an elevational gradient

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Abstract: Aim Mountains are biodiversity hotspots and are among the most sensitive ecosystems to ongoing global change being thus of conservation concern. Under this scenario, assessing how biological communities vary over time along elevational gradients and the relative effects of niche-based deterministic processes and stochastic events in structuring assemblages is essential. Here, we examined how the temporal trends of bird communities vary with elevation over a 20 year-period (1999–2018). We also tested for differences in temporal dynamics among habitat types (among-community variability) and functional groups (within-community variability). Taxon 97 species of common breeding birds. Location Swiss Alps. Methods We used abundance data from the Swiss breeding bird survey to compute different temporal dynamic metrics (temporal turnover, synchrony, rate of community change and community-level of covariance among species). We also examined the relative contribution of deterministic and stochastic processes in community assembly using the Raup-Crick method and the normalized stochasticity ratio. Results We found that, with greater elevation, temporal species turnover increased while the rate of overall community change over successive years decreased, suggesting that high-elevation communities display more erratic dynamics with no clear trend. Despite this, we found a more deterministic assembly of alpine communities in comparison to those located at lower elevations. Deterministic processes had greater influence than stochastic processes on community assembly along the entire elevational gradient (80% of communities). Forest communities exhibited higher synchrony in comparison to the remaining habitats likely because they consisted of species with greater functional redundancy, whereas alpine communities were the least stable as a result of their low taxonomic richness ('portfolio' effect). Main conclusions Community-level synchrony was overall positive supporting the idea that compensatory mechanisms are rare in natural biological communities. Our results suggest that rather than competition, the existence of differences in the ecological strategies of species may have a stabilizing effect on bird communities by weakening the concordance of species responses to fluctuations in environmental conditions (i.e. enhanced interspecific temporal asynchrony). This study provides evidence that, although species turnover in meta-communities is frequent, a high temporal turnover does not necessarily imply the overriding importance of stochastic processes.

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**Spatial heterogeneity in temporal dynamics of Alpine bird communities
along an elevational gradient**

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Running head: Temporal dynamics of bird communities

Abstract Aim: Mountains are biodiversity hotspots and are among the most sensitive ecosystems to ongoing global change being thus of conservation concern. Under this scenario, assessing how biological communities vary over time along elevational gradients and the relative effects of niche-based deterministic processes and stochastic events in structuring assemblages is essential. Here, we examined how the temporal trends of bird communities vary with elevation over a 20 year-period (1999-2018). We also tested for differences in temporal dynamics among habitat types (among-community variability) and functional groups (within-community variability). Taxon: 97 species of common breeding birds. Location: Swiss Alps. Methods: We used abundance data from the Swiss breeding bird survey to compute different temporal dynamics metrics (temporal turnover, synchrony, rate of community change, and community-level of covariance among species). We also examined the relative contribution of deterministic and stochastic processes in community assembly using the Raup-Crick method and the normalized stochasticity ratio. Results: We found that, with greater elevation, temporal species turnover increased while the rate of overall community change over successive years decreased, suggesting that high-elevation communities display more erratic dynamics with no clear trend. Despite this, we found a more deterministic assembly of alpine communities in comparison to those located at lower elevations. Deterministic processes had greater influence than stochastic processes on community assembly along the entire elevational gradient (80% of communities). Forest communities exhibited higher synchrony in comparison to the remaining habitats likely because they consisted of species with greater functional redundancy, whereas alpine communities were the least stable as a result of their low taxonomic richness ('portfolio' effect). Main conclusions: Community-level synchrony was overall positive supporting the idea that compensatory mechanisms are rare in natural biological communities. Our results suggest that rather than competition, the existence of differences in the ecological strategies of species may have a stabilizing effect on bird communities by weakening the concordance of species responses to fluctuations in environmental conditions (i.e., enhanced interspecific temporal asynchrony). This study provides evidence that, although species turnover in metacommunities is frequent, a high temporal turnover does not necessarily imply the overriding importance of stochastic processes.

61

62 **Introduction**

63 The richness and composition of biological communities, termed community structure, changes
64 through time as a result of population fluctuations as well as local colonizations and extinctions of
65 species (species turnover; Legendre & Gauthier, 2014). Both abiotic and biotic factors are responsible
66 for generating instabilities that lead to either directional (predictable) or non-directional changes in
67 species assemblages. Directional changes imply a general pattern in response to a meaningful
68 disturbance or a perturbation that extends over time (e.g., progressive habitat change linked to land
69 use change or long-term climate trends) (Dornelas et al., 2014; Hoover et al., 2014). These are driven
70 by deterministic processes that involve non-random, niche-based mechanisms including
71 environmental filtering and interspecific interactions (Vellend, 2016). In contrast, erratic fluctuations
72 may arise as a consequence of stochastic processes (e.g., ecological drift or unpredictable weather
73 events like hurricanes) without a particular direction (Renner et al., 2014). Under certain
74 circumstances, community structure remains stable over long time periods ('loose equilibrium')
75 despite the existence of annual fluctuations in composition and abundance (Collins, 2000). The
76 capacity of communities to rebound from perturbations and persist over time is known as community
77 stability. This property informs us about the potential resilience of species to disturbances such as
78 biological invasions (Elton, 1958; Loreau et al., 2002; Tilman et al., 2006). Consequently, assessing
79 how communities vary over time and the relative effects of deterministic and stochastic processes in
80 structuring assemblages is highly relevant from a conservation perspective, particularly in the face of
81 climate change which is characterized by increasingly extreme weather events (Buckley et al., 2018).

82 Community stability is largely dependent on the degree of synchrony in population
83 fluctuations of its constituent species. The lower the degree of similarity in year-to-year fluctuations
84 among species, the greater the stability of the community ('insurance effect': Yachi & Loreau, 1999).
85 Community synchrony can be affected by external factors, such as disturbances (e.g., habitat
86 degradation as result of land use changes), which can lead to long-term directional trends in species
87 composition, and by internal properties of the community like the strength of interspecific

competition. Regarding this, competition among species is generally expected to increase asynchrony, leading to compensatory dynamics where fluctuations in the density of one species are offset by the opposite fluctuations of (an)other species (González & Loreau, 2009). Therefore, communities with high functional diversity (i.e., those composed of species with different ecological strategies) should be more likely to exhibit a higher level of asynchrony, and thus higher stability than functionally poor assemblages ('portfolio effect': Doak et al. 1998). In addition to community synchrony, several other metrics have been devised in order to quantify how communities change in response to environmental drivers; that is, if they remain invariant, if they gradually track these changes or, instead, they shift abruptly exhibiting early warning signals of ecological collapse (Gauzère et al., 2015; Blüthgen et al., 2016; Spanbauer et al., 2016). For instance, Collins et al. (2008) employed the rate of compositional change to compare the temporal dynamics of plant species in burned *versus* unburned areas at the Konza Prairie Long-Term Ecological Research (LTER) site.

Environmental gradients have been frequently employed to examine the influence of varying environmental conditions on community assembly (e.g., Cornwell & Ackerly, 2009). The relative influence of biotic and abiotic factors on community composition varies along such gradients of environmental stress or resource availability. For instance, the relevance of competitive interactions tends to decline with environmental harshness (Travis et al., 2006), whereas the role of abiotic factors (e.g., elevation or mean temperature) as drivers of biodiversity is generally more important in severe environments (Kraft et al., 2015; Jarzyna et al., 2019). However, the relationship between temporal patterns in community dynamics and environmental drivers has received minimal attention (e.g., Blüthgen et al., 2016). Although temporal patterns are often assumed to be relatively homogeneous across a landscape, spatial variation in ecological conditions may create heterogeneity in the temporal dynamics of communities (Devictor et al., 2008; Spotswood et al., 2015; Dencker et al., 2017; Beukhof et al., 2019). For instance, habitats with lower carrying capacity like alpine grasslands and other low-productivity ecosystems may exhibit higher turnover in community composition compared to environments supporting large populations, mainly due to increased demographic or environmental stochasticity (Jarzyna & Jetz, 2017). Likewise, not all components of a given community necessarily respond in a similar way, and consequently, certain taxonomic groups or ecological guilds may be

more likely to exhibit signatures of directional change than others (Kampichler et al., 2012). Regarding the latter case, in another study carried out at the Konza LTER site, Jones et al. (2017) reported that grasshopper and small mammal communities were stable, whereas bird communities underwent directional change driven to some extent by stochastic processes. It is likely that this has to do with the fact that the food resources on which birds depend -insects- are more unpredictable from one year to the next.

Here, we study spatial heterogeneity in the temporal dynamics of bird communities in the Swiss Alps. The main goal was to examine how temporal trends in community structures vary along an elevational gradient. Elevation is typically the main agent driving species assembly in montane communities, and, consequently, a plethora of studies have addressed how the compositional, functional, and phylogenetic structure of ecological communities varies with elevation (e.g., Graham et al. 2009; Machac et al., 2011; Dehling et al., 2014; see also García-Navas et al., 2020). Nevertheless, few studies have looked at the relationship between elevation and the trajectories that communities exhibit over time, which, in turn, may affect the stability and temporal variability of communities (Jarzyna et al. 2015, 2016; Gaüzère et al., 2017). We also tested if the influence on elevation of these metrics differed among different habitat types (forests; farmlands; mixed and alpine habitats) nested within the elevational gradient (among-community variability) and tested for differences in temporal dynamics among functional groups (within-community variability). Specifically, we tested the following predictions, which are summarized in Fig.1a: [i] since high-elevation communities are typically composed of (a) mountain specialists whose populations tend to be relatively stable and (b) generalists expanding their distribution range upwards and undergoing marked population fluctuations (Zamora et al., 2017), we predict a higher temporal turnover in alpine environments; [ii] since environmental adversity at high-elevation sites results in limited functional trait diversity and functional convergence (functional clustering; García-Navas et al., 2020), we predict the existence of higher temporal synchrony in alpine communities in comparison to communities at lower elevations; [iii] since forests are more predictable environments and thus, more likely to remain unaltered over time in comparison with farmlands and alpine habitat as a result of management (e.g., Burel et al., 2013) and more variable conditions (e.g., landslides and snowslides),

we predict a higher stability in forest bird communities compared to those from farmlands and alpine habitats; and [iv] since it has been hypothesized that deterministic processes inherent in niche-based theories of community assembly predominate in lower-productivity systems and stochastic processes are more prevalent in high productivity systems due to differential colonization history (Chase, 2010), we predict that the relative contribution of deterministic vs. stochastic processes increases with elevation.

Material and Methods

Data collection

We compiled data from the ‘Monitoring Häufige Brutvögel’ (MHB) scheme, a volunteer-based programme aimed at annual monitoring of population dynamics of common breeding species in Switzerland, a small country (41,285 km²) in Western Europe. This programme started in 1999 and follows a standardized territory mapping protocol in which 267 1×1 km plots from a regular grid covering the entire country are surveyed 2-3 times by skilled birdwatchers during the breeding season (15th april-15th June). Observers record every bird seen or heard along a square specific transect route (~5-km long) that does not change over the years (for more details see Schmid et al., 2004; Kéry & Royle, 2009). In this study, we restricted our analysis to the region of the Alps (60% of Switzerland; ~25,000 km²), and selected those plots that have been uninterruptedly surveyed from 1999 to 2018. Observations of the two or three visits were grouped into territories using “TerriMap” (Schmid, 2017). Thus, our dataset consisted of relative abundance data (number of territories per site) collected during two decades in 131 plots along a ~2,300 m elevational gradient (range: 380-2,710 m). Study plots were classified into four different habitat categories (forest; farmland; mixed; alpine) according to the predominant land use (see Table 1 and Fig. 1b). Land use information (geostat data at 1×1 km² resolution) was obtained from an aerial survey carried out by the Swiss Federal Office for Statistics (Arealstatistik; www.bfs.admin.ch). Waterbirds, nocturnal birds and raptor species with large home ranges were excluded from the dataset as they are not properly surveyed by the programme. In total,

97 common breeding species (accounting for about 99% of the abundance data) were included in the analyses.

Quantifying temporal dynamics

In order to test our first prediction (prediction [i] in Fig. 1a), we computed an estimate of temporal turnover defined as the proportion of species that differ between consecutive years ([number of species gained + number of species lost]/total number of species observed in both years) (i.e., richness-based species exchange ratio *sensu* Hillebrand et al., 2018; see also Cleland et al., 2013). We also calculated the number of species that appeared ('gains') and disappeared ('losses') in t_1 relative to total species richness across both time points, t_{-1} and t_1 .

We then distinguished between directional and non-directional change by estimating the rate of community change over the study period for each plot. This metric quantifies the rate and direction of change in a given community (time-lag analysis; Collins et al., 2000; Hallett et al. 2016). It is calculated by regressing Euclidean distances arising from pair-wise communities on the time-lag interval (i.e., plots are compared to themselves across years in terms of species composition). A positive-sloped relationship indicates that a given community is increasingly dissimilar over time (i.e., it veers away from its original state directionally driven by internal or external factors or due to autocorrelated stochastic variability). Also, it means that there is a high proportion of species with stochastic dynamics or directional change. A slope close to zero indicates that abundances of the constituent species oscillate around a constant mean over time or that local populations show high lability and they randomly disperse or disappear according to a white noise process, which means that the abundance of a species at a given time (t_1) is partly or completely independent of the previous state (t_0) (i.e., high stochasticity; Kampichler & van der Jeugd, 2013). Significant negative slopes indicate convergent behavior; for instance, the return of the community to an earlier state in the time series (Kampichler et al., 2014). In this way, we tested whether in a given community species are continually reshuffled at random or there is a progressive succession of species so that the resulting species composition differs greatly from the original one.

Complementarily, we split our abundance data into different subsets according to the foraging niche (aerial; arboreal; ground; and generalist) and diet (insectivorous; granivorous, frugivorous and/or herbivorous; carnivorous and/or scavenger; and omnivorous) of species. Foraging niche and diet (feeding group) categories were assigned following Storchová & Hořák, (2018). In this way, we assessed if different components of the community are responding in similar or different ways over time.

Estimating extinction rates

We estimated extinction rates for each plot (i.e., for the entire community) and for the two main guilds (arboreal- and ground-foragers) and feeding groups (insectivorous and granivorous-frugivorous-herbivorous) separately, by using the R package *island* (Ontiveros et al., 2019). This package follows the stochastic implementation of Simberloff's model (1969) inspired by the theory of island biogeography (MacArthur & Wilson, 1967) and developed by Alonso et al. (2015) to estimate colonization and extinction rates for communities that have been repeatedly sampled through time by means of a likelihood approach. We do not report colonization rates as preliminary analyses showed that the probability of colonization heavily depends on the number of species not detected across two time periods and thus, on the species pool, which vary among plots. That is, colonization rates are not comparable among communities as they are computed in relation to the number of missing species in each plot. Meanwhile, extinction rates are computed with respect to the number of species occurrences and are independent from the overall species pool. Consequently, we could not calculate a relationship between colonization rates and 'gains' (i.e., number of species that appeared in t_1 relative to $t_0 + t_1$), whereas we found a strong relationship between extinction rates and 'losses' (i.e., number of disappearances) ($\rho = 0.98$, $p < 0.001$).

Quantifying community stability

In connection with the second prediction (prediction [ii]) we quantified the degree of synchrony in species abundances within each plot over time. Despite the existence of strong fluctuations in species' population sizes, communities may remain stable if increases of certain species are accompanied by

compensating declines in other species. That being so, it should translate into a great level of asynchrony among species over time and the existence of negative covariance among population abundances in a given community (Yachi & Loreau, 1999). We first quantified the level of synchrony in species abundances within a community over time using the approach proposed by Loreau & Mazancourt (2008). This measure of synchrony (φ), which oscillates between 0 (total asynchrony) and 1 (total synchrony), compares the variance of aggregated species abundances with the summed variances of individual species:

$$\varphi = \frac{\sigma(\chi_T)^2}{(\sum_i \sigma_{\chi_i})^2}$$

where:

$$\chi_T(t) = \sum_{i=1}^N \chi_i(t)$$

Thereby, we assessed how changes in taxon abundances within a community track one another over time. Complementarily, we used two additional measures of species synchrony; η (Gross et al., 2014) and its modified version, η_w (Blütghen et al., 2016), in which species are weighted by their relative total abundances over all years. Both, η and η_w were compared with the null model of independence of species fluctuations (η or $\eta_w = 0$) and oscillate between -1 and 1, with negative values indicating compensatory dynamics and positive values (partial) synchrony.

Next, we calculated a community-level measure of species covariance, the log-transformed Schluter' variance ratio, in order to test for negative covariance among species (i.e., compensatory dynamics) (Schluter, 1984; Lepš et al., 2018). The variance ratio (VR) compares the variance of the community as a whole relative to the sum of individual population variances (Peterson, 1975; Houlahan et al., 2007). Negative values of log VR indicate that species tend to co-vary negatively, suggesting the existence of 'compensatory dynamics' (i.e., increases/decreases in some species are partly compensated for by decreases/increases in others). Positive values of VR indicate that species generally positively co-vary, suggesting the existence of 'synchronous dynamics' (i.e., community variability is greater than expected under the assumption of species independence) (Lepš et al., 2018).

Complementarily, to test whether variance ratios significantly differed from what is expected at random, we used a temporal modification of the torus translation (Harms et al., 2001) in which we randomly selected a different starting year for each species' time series following Hallet et al. (2014). This randomization procedure generates a null community matrix in which species abundances vary independently whereas within-species autocorrelation is kept constant. The null distribution was obtained after 10,000 cyclic shift permutations.

Further, we disentangled the effect of directional trends and similarity in year-to-year fluctuations on synchrony indices following two methods recently developed by Lepš and collaborators (2019). The rationale behind this analysis is that long-term directional trends in species composition due to land-use or climate change can lead to an apparent increase in synchrony that is not due to concordant fluctuations in species abundances. To filter out the pervasive effects of directional trends, Lepš et al. have proposed two solutions. The first approach is applicable to the above-mentioned synchrony indices and consists of applying the three-term local variance ($T3$). That is, variance is not computed as the average of squared deviations from the overall mean, but from the squared difference of the middle year (t_0) and average of the year before (t_{-1}) and after (t_{+1}) within a movable 3-yr window (Lepš et al., 2019). The second approach is based on computing synchrony over the residuals of fitted species trends over time. Thereby, it is possible to decompose synchrony into the part that can be ascribed to the directional trend and the part that is due to residual variation (i.e., detrended component) (i.e., $S_{\text{total}} = S_{\text{trend}} + S_{\text{detrended}}$). Thus, for each plot we estimated the $T3$ version of each synchrony index (ϕ , η and η_w) and decomposed total synchrony into two components: the one caused by the trend and the one arising from year-to-year fluctuations.

Lastly, in order to test the third prediction (prediction [iii]), we used the stability of summed species abundances defined as the temporal mean divided by the temporal standard deviation (i.e., the inverse of community variability, $CV = \sigma/\mu$) as an estimate of community stability (Tilman, 1999). We calculated an overall estimate of community stability and community asynchrony for each plot. In addition, we calculated eight complementary estimates after classifying species by ecological guild and feeding group in a similar way to that described above.

Deterministic vs. stochastic processes

In order to disentangle the relative contribution of deterministic (i.e., niche-based mechanisms including environmental filtering) and random (e.g., ecological drift) processes in community assembly and examine whether our fourth expectation (prediction [iv]) was fulfilled, we applied two methods: a null model-based approach, the Raup-Crick metric, developed by Chase et al. (2011) over Raup & Crick (1979)'s original idea, and a mathematical framework with an associated normalized index, the normalized stochasticity ratio (NST), recently devised by Ning et al. (2019) with microbial data.

Raup-Crick (β_{RC}) is robust to variations in local species richness and expresses the compositional dissimilarity between the observed communities relative to those generated under a null model. Thus, this method evaluates the role of deterministic *vs.* stochastic processes while controlling for differences in α -diversity among localities. β_{RC} values indicate whether two given communities are more dissimilar (approaching 1), as similar (approaching 0) or less dissimilar (approaching -1) than expected by random processes. The null expectation was generated using 1,000 iterations.

The NST method measures the relative position of observed values between the extremes under pure deterministic and pure stochastic assembly. NST ranges from 0 to 100%, with 50% being the boundary point between more deterministic (<50%) and more stochastic (>50%) assembly. See Ning et al. (2019) for an explanation of the equation employed to compute the NST ratio and additional mathematical details.

Community composition

As final step, in order to visually assess differences in community composition among habitat types, we used the 'betadisper' function, which implements Anderson (2006)'s procedure for the analysis of multivariate homogeneity of group dispersions (variances). This procedure plots dissimilarity between sampling groups using principal coordinates analysis and reduces the original multidimensional space to a 2-D space. We then determined if communities differed statistically among habitat types using permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarities

(Anderson, 2001). We used the function ‘envfit’ to test the significance of the relationship between elevation and community structure. This function tests the significance of environmental factors using squared correlation coefficients as a goodness-of-fit following 999 permutations and providing empirical *p*-values. We then used ‘ordisurf’ to illustrate relationships in bird communities to changes in elevation. This function fits a smooth surface for continuous variables onto the ordination plot with cross-validatory selection of smoothness.

Statistical analyses

We used generalized linear models to test the effect of elevation on the different metrics of temporal dynamics (namely; temporal turnover, number of appearances (‘gains’) and disappearances (‘losses’), rate of change, synchrony and community stability estimates, and relative contribution of stochasticity). As the relationship between elevation and the response variable does not necessarily have to be linear, we also built polynomial models (including a quadratic or cubic term). We further tested for habitat differences in the above-mentioned metrics using one-way ANOVA.

Complementarily, we analyzed both factors, elevation and habitat, jointly. Despite the relationship between our response variable and elevation being non-linear in several cases (see *Results*) and habitats were not evenly distributed along the elevation gradient, when both factors were analyzed together we did not find a significant elevation×habitat interaction in most cases (see Table S1). This means that the slope of the relationship between the response variable and elevation does not change direction based on the habitat type. Consequently, we examined the main effects using Type-II sums of squares (only in those cases in which the elevation×habitat interaction was significant, we applied Type-III ANOVA). For the sake of brevity, these results are only shown in Supplementary Material. Lastly, we also examined whether these metrics differed between guilds within the same plot by means of paired *t*-tests.

All analyses were carried out in the R environment (R v. 3.5.2.; www.r-project.org) using the libraries *car* (Fox & Weisberg, 2019), *vegan* (Oksanen et al., 2013), *codyn* (Hallett et al., 2016), *island* (Ontiveros et al., 2019) and *nst* (Ning, 2019).

Results

Temporal dynamics

Turnover rates between adjacent years averaged 26.3% ($\pm 6.0\%$, range from 6.2 to 43.6%). The turnover rate tended to increase with elevation up to 2,000 m, although a few localities in the lowlands (most of them located in the Northern Alps) exhibited above average values leading to a sigmoidal pattern (Fig. 2a). There were statistically significant differences among habitat types in terms of gains, losses, and turnover rate (Table 2). Both the proportion of species that disappeared and the proportion that appeared were higher in alpine localities compared to the remaining habitat types, highlighting the dynamic nature of these high-elevation environments (Table 2).

The rate of community change decreased with elevation (Fig. 2b). Communities located in mixed habitats displayed the fastest change (i.e., steepest slopes), which suggests that these bird assemblages were increasingly dissimilar over time (Table 2). Meanwhile, alpine environments showed the shallowest time-lag analysis (TLA) slopes, suggesting low directionality in compositional changes of species assemblages inhabiting these environments, in which species appeared and disappeared in a more erratic way. When assessing species exploiting different resources, we found that the arboreal and insectivorous guilds showed steeper TLA slopes ($b = 0.41$ and 0.53 , respectively) in comparison to the ground-foraging and plant-and-seed-eating guilds, respectively ($b = 0.34$ and 0.16).

Extinction

The mean value of extinction for all species was $0.19 (\pm 0.05)$, which indicates that on an average survey plot, approximately 19% of species of the original assemblage had become extinct. Estimated extinction rates differed among habitat types (farmland: 0.18 ± 0.05 , mixed: 0.17 ± 0.02 , forest: 0.18 ± 0.05 , alpine: 0.22 ± 0.07 ; $F_{3,126} = 9.50$, $p < 0.001$) and increased from 1,500 up to 2,000 m, from which a sharp decrease was found (see Fig. S1). Extinction rates estimated separately for arboreal

species increased positively with elevation, whereas extinction rates of ground-foragers tended to adopt a quadratic pattern (Fig. S2). On the contrary, extinction rates for insectivorous and plant-and-seed-eating guilds did not correlate with elevation (both p -values >0.05). Estimated extinction rates were higher for the herbivorous group (plant, fruit, and seed eaters) in comparison with those obtained for the insectivorous guild (0.34 ± 0.16 vs. 0.18 ± 0.06 ; paired t -test: $t = -10.59$, $p < 0.001$). There were no significant differences in probability of extinction between arboreal and ground-foraging guilds (0.22 ± 0.15 vs. 0.21 ± 0.08 ; $t = -0.62$, $p = 0.53$).

Synchrony and community stability metrics

The four synchrony measures used (φ , η , η_w and $\log VR$) were all positively correlated (see Table S2), but only φ was significantly correlated with elevation ($t = 2.23$, $p = 0.03$) probably due to this index being more sensitive to species richness variation than the others (Table S2). However, the polynomial (cubic) model provided a better fit than the linear one (Table 3; Fig. S3). The variance ratio (VR) among species was quadratically related to elevation with maximum values around 1,000-1,500 m (Table 3; Fig. 3). Most plots (87%) exhibited VR values higher than expected by chance and only two presented a negative covariance. All synchrony indices except η differed significantly among habitat types (Table 3). Forest assemblages exhibited the highest values of synchrony and covariance. Alpine, farmland, and mixed habitats showed quite similar values of synchrony, but the variance ratio ($\log VR$) was much lower in alpine environments in comparison to the remaining categories (Table 3). Alpine and forest communities also exhibited the lowest values of stability, which decreased with elevation (Table 3). On the contrary, mixed habitats harbored the most stable communities (Table 3).

We did not find statistically significant differences in degree of community synchrony (estimated as φ) between the arboreal and the ground-foraging guild (0.22 ± 0.13 vs. 0.23 ± 0.12 ; paired t -test: $t = 0.57$, $p = 0.56$) or the insectivorous and the plant-and-seed-eating guild (0.25 ± 0.14 vs. 0.24 ± 0.11 ; $t = -0.73$, $p = 0.46$). However, in terms of community stability, we observed that the ground-foraging guild and the insectivorous guild are more stable than the arboreal and the plant-and-

seed-eating guilds, respectively (ground vs. arboreal: 4.98 ± 1.77 vs. 2.46 ± 1.00 ; $t = 14.48$, $p < 0.001$, insectivorous vs. plant-and-seed-eating: 5.64 ± 2.16 vs. 3.12 ± 1.10 ; $t = -14.57$, $p < 0.001$).

When using the three-term local variance ($T3$) approach to filter out the pervasive effects of directional trends on synchrony, we obtained very similar results to those described above; forests harbored the most synchronous communities, although differences between alpine communities and the remaining habitat types were slightly larger (see Table 3). Accordingly, when decomposing synchrony values, we found that habitat differences in synchrony were not governed by differences in directional trends (S_{trend}), which did not differ significantly among habitat categories ($F_{3,126} = 2.51$, $p = 0.062$). Habitat differences in species year-to-year fluctuations ($S_{\text{detrended}}$) were significant ($F_{3,126} = 12.17$, $p < 0.001$); forest and alpine communities exhibited the greatest and smallest values of detrended synchrony, respectively (Fig. 4a). $S_{\text{detrended}}$ was quadratically related with elevation (Fig. 4a; elevation: $t = 2.78$, $p < 0.01$, elevation²: $t = -3.52$, $p < 0.001$), whereas S_{trend} showed a less pronounced (non-significant) ‘hump-shaped’ pattern (Fig. 4b). The proportion of communities exhibiting negative S_{trend} values indicative of successional dynamics was much higher (about double) in mixed habitats compared to other categories (Table 4).

Deterministic vs. stochastic processes

The Raup-Crick null-based approach allowed us to estimate the magnitude to which beta (β) diversity deviated from the expectation under a random assembly process while taking differences in species richness and relative abundance into account (i.e., beta-deviation, β_{RC}). β_{RC} values adopted a sigmoid curve along the elevational gradient; alpine communities were more dissimilar than expected by chance (i.e., more distant from null expectations) relative to mid-elevation communities, suggesting that changes in β -diversity were not simply due to a random influence of elevation on species in each locality, and instead likely due to elevation acting as an environmental filter (elevation: $t = -2.04$, $p = 0.04$; elevation²: $t = 2.21$, $p = 0.03$; elevation³: $t = -2.33$, $p = 0.04$; Fig. 5a). Alpine communities had greater β_{RC} values compared to the rest of the habitats (alpine: 0.093 ± 0.04 , forest: 0.064 ± 0.02 , farmland: 0.066 ± 0.02 , mixed: 0.060 ± 0.02 ; $F_{3,126} = 11.36$, $p < 0.001$).

Most communities (80%) showed normalized stochasticity ratio (NST) values <50% indicating the prevalence of deterministic assembly. Alpine communities presented half as large NST values (19.7%) compared to the remaining habitats (forest: 40.5, farmland: 47.2, mixed: 48.3%) ($F_{3,125} = 37.13, p < 0.001$). Accordingly, the relative importance of stochastic processes in governing community diversity decreased with elevation after reaching its maximum around 1,500 m (elevation: $t = 3.19, p < 0.01$; elevation²: $t = -5.45, p < 0.001$; Fig. 5b).

Community composition

The PERMANOVA analysis showed significant differences among habitat types ($R^2 = 0.44, F = 678.01, p = 0.001$) and study year ($R^2 = 0.01, F = 6.35, p = 0.002$), and a habitat $\times$ year interaction ($R^2 = 0.01, F = 2.58, p = 0.015$). Bird communities belonging to different habitat types occupied a different region in the 2-D ordination space (Fig. 6). Almost all the space occupied by communities from mixed habitats overlapped that of forest and farmland assemblages, whereas alpine communities conformed a cluster with the highest level of spatial separation (Fig. 6). When we fitted elevation as environmental vector onto the ordination space, we observed that this factor explained a significant proportion of the variance ($r^2 = 0.81, p = 0.001$). We obtained a similar result when fitting elevation as smoothed surface using a Generalized Additive Model (GAM) ($R^2 = 0.88, t = 429.2, p < 0.001$; see inset in Fig. 6).

Discussion

Here, we provided evidence that high-elevation bird communities in the Alps exhibit a higher turnover rate and limited directional change in composition over time despite the predominance of niche-based, deterministic processes in community assembly. Communities at mid- and low-elevations are increasingly more dissimilar over time, particularly in mixed habitats where successional dynamics are more likely to occur (e.g., open-habitat specialists progressively colonizing woodland edges and forest glades). The role of stochastic assembly was greater at low- and mid-

elevation than at higher elevations, but deterministic processes had a predominant role in structuring bird communities along the entire elevational gradient.

Indices of temporal dynamics and extinction rates

Communities located at higher elevation displayed greater number of species gains and losses, and consequently a higher turnover rate. Many alpine localities were occupied by the same species only for one or two years before being abandoned, only to be recolonized later, indicating a high instability in these communities (Knaus et al., 2018). On the contrary, farmland communities exhibited the lowest numbers of both appearances and disappearances of new species. The low extinction rate is striking as in Switzerland (as in other regions of Europe) farmland bird populations have experienced marked declines in recent decades (55% on average for the period 1990-2018; Knaus et al., 2019), but the regions in which these were steepest, for instance the Central Plateau, were not included in this study. This suggests that trends observed at community level do not mirror those observed at an individual species level, which may be due to the existence of compensatory mechanisms or lags in the response of communities to disturbances (Supp & Ernest, 2014).

The most probable reason for more dynamic communities occurring at high elevation (around 1,800-2,000) is that a substantial proportion of species present in these assemblages are close to their physiological limits and their populations are therefore more vulnerable to fluctuations in abiotic conditions, which gives rise to a high temporal turnover (e.g., Sexton et al., 2009; Londoño et al., 2017). Accordingly, we observed that extinction rates increased from 500 to 2,000 m, reinforcing the idea that increasing environmental harshness makes local populations more susceptible to extinction or more prone to move in search of more benign conditions (McCain, 2009). Thus, communities at high elevation are largely made up of species that come and go uninterruptedly as they are at their range boundaries (Sekercioglu et al., 2008). In this sense, there is evidence that some species in the Swiss Alps and other mountain systems are shifting their upper elevational limit in response to the upward advancement of the treeline (e.g., Harsch et al., 2009; Vittoz et al., 2013; Freeman et al., 2018). Nevertheless, although these shifts occur from one year to the next, they take time to consolidate and perpetuate over the years. Above the natural treeline (>2,100 m) only a small subset

of taxa adapted to high-elevation conditions (bare rock, permanent snow) are able to subsist. They are high mountain specialists (e.g., snow finch *Montifringilla nivalis*) as they live only near mountain summits, and thus their populations are more stable in comparison to that of generalist species colonizing new elevation levels (e.g., tree pipit *Anthus trivialis*; alpine accentor *Prunella collaris*; European robin *Erithacus rubecula*, see Knaus et al., 2018) (Kolasa & Li, 2003). In addition, species conforming these high-elevation communities tend to exhibit lower reproductive rates, lower survival prospects, and lower dispersal capacity, which would make them less resilient to environmental change (García-Navas et al., *submitted*).

Our time-lag analyses showed that the slope resulting from plotting pairwise temporal dissimilarity values against temporal distances between samples decreased with increasing elevation, suggesting that the way communities change over time varies along an elevational gradient. Time-lag analysis (TLA) revealed an increase in dissimilarity with increasing time lag in lowland communities, mainly those located in mixed habitats (open and successional forests, edge habitats). These transition environments may harbor a considerable number of ‘directional’ species (species that were present earlier, but later become locally extinct or colonizing species that enter the community later and continually increase their abundance). Conversely, alpine communities showed the shallowest slopes, which suggests a more erratic nature (no temporal autocorrelation) of species assemblages in this habitat. The low densities of many alpine species may lead to stochastic disappearances and reappearances. In addition, it may also be due to these assemblages being composed of a mixture of constant species and species that have more erratic or directional species with low temporal variability (Kampichler & van der Jeugd, 2013). Our results agree with those reported by Kampichler et al. (2014) in a comparative analysis of bird communities from a variety of terrestrial ecosystems, from primeval to disturbed forests. They reported that, although the slope, and thus the rate of community change, varied widely among localities (with lowest and highest values for Białowieża’ pristine forests and successional forests, respectively), all assemblages showed significant directional change of community composition (Kampichler et al., 2014). Thus, TLA can yield significant slopes for communities characterized by remarkably different dynamics, and only those communities that are almost entirely composed of species with constant population sizes or those whose species

abundances are driven by a pure white noise process are differentiated from the rest. The observation of shallowest slopes in high elevation environments (alpine meadows) may also have to do with the lower proportion of foliage-gleaning species that can be found in these habitats in comparison with those at lower elevations. When discerning between species guilds, we found that arboreal species and insectivorous species showed steeper slopes than ground-dwelling and herbivorous guilds suggesting that guilds that heavily depend on trees may *a priori* exhibit less steady population dynamics.

Temporal synchrony and community stability

We failed to detect a significant linear relationship between elevation and most indices of community synchrony. It may be due to the existence of habitat-specific differences and variations in the representation of each habitat type along the elevational gradient (see Table 1). Temporal synchrony analysis indicated that species in forest communities are more synchronous than those in the remaining habitats probably as a result of differences in magnitude and duration of resource pulse events. Whereas farmlands, mixed and alpine habitats are unlikely to exhibit large interannual differences in food resources for birds inhabiting these ecosystems, forests are more prone to display huge variations in resource availability (insects, fruits, seeds) from one year to the next. It occurs as a result of fluctuations in mast production and cyclic or non-cyclic caterpillar outbreaks, which initiate cascades of direct and indirect effects that permeate throughout forest communities (e.g., Schmidt & Ostfeld, 2003; Clotfelter et al., 2007). Regarding this, there is evidence that fluctuating resource availability increases community synchrony and temporal variability (i.e., the inverse of temporal stability) (Li & Stevens, 2017). Although resource availability seems to play a central role in regulating species responses and how they fluctuate in relation to the rest of the community, intrinsic properties of assemblages can also have influence on the level of community-wide synchrony. For instance, according to theory-based expectations (Morin et al., 2014), taxa with different ecological strategies should fluctuate less synchronously than more similar taxa; however, the relationship between functional diversity and community synchrony have been barely explored (but see Klink et al., 2019). Hence, it is likely that low functional originality and functional divergence in forest assemblages (García-Navas et al., 2020) contribute to the concordance of species responses to

environmental fluctuations (e.g., inter-annual climatic fluctuations). Thus, even though most bird species breeding in temperate systems exhibit a similar response to favorable and unfavorable environmental conditions (e.g., most species show higher fitness in warm springs with sufficient precipitation), the level of functional resemblance among species may boost or dampen the influence of environmental filtering on community synchrony (Loreau & de Mazancourt, 2008; Adler et al. 2013). Another factor that can either increase or decrease the level of synchrony is the directional change in species composition. For instance, successional changes after some disturbance (e.g., fire or human-induced deforestation) can catalyze community change in a directional way, masking the effect of year-to-year variation (Chapin III et al., 2006; Pandit et al., 2013). When filtering out the effects of directional trends, we observed that the level of synchrony of alpine communities decreased slightly with respect to that of other categories. However, results remained quite similar; the higher synchrony level observed in forest communities cannot be attributed to the existence of habitat-specific long-term directional trends. In fact, when decomposing overall synchrony into trend (S_{trend}) and detrended (S_{detrend}) synchrony, we observed that S_{trend} dampens differences in year-to-year variation among habitats.

Since community stability and synchrony were negatively correlated, the less stable communities were those located in forests and alpine habitats. On the contrary, farmlands and mixed habitats exhibited the highest community stability values. Our results thus do not support the idea that habitat conversion and historical deforestation result in reduced diversity and asynchrony (*cf.* Blüethgen et al., 2016). It may be due to agriculture in Switzerland being largely dominated by small farms, mostly in the Alps where traditional and agri-environmental practices are more common than in other regions (Jura region and Central Plateau) (BAFU, 2017). Regarding this, theoretical studies have suggested that interspecific competition may stabilize biological communities by enhancing negative covariation in relative abundances of the constituent species (e.g., González & Loreau, 2009). However, here we only found two plots with negative covariance values, supporting the view that compensatory dynamics are rare in natural biological communities (Houlahan et al., 2007; Valone & Barber, 2008; but see Hallett et al., 2014). The level of asymmetry between coexisting species seems to constitute a more important factor in terms of community stability. By weakening

interspecific temporal synchrony, species functional dissimilarity may have contributed to stabilize communities in farmlands and mixed habitats. Although the alpine communities presented values of synchrony similar to those observed in farmland and mixed-habitat communities, the average level of stability was even lower than that reported for forests. Such a discrepancy probably arises as result of lower taxonomic richness of alpine environments, since temporal stability at the community level cannot be achieved solely by higher asynchrony across species ('insurance effect'; Naeem & Li, 1997; Yachi & Loreau, 1999), but also by higher species diversity (the so-called 'portfolio effect'; Doak et al., 1998). The negative relationship between community stability and elevation provides support for the notion that species richness acts as a buffer against environmental perturbation, which is highly relevant in conservation terms (Tilman, 1999; García-Palacios et al., 2018; Joseph et al., 2019).

Deterministic vs. stochastic processes

The relative influence of deterministic *versus* random processes in community assembly varied along the elevational gradient, with stochastic factors being more influential in low-elevation communities. Raup-Crick β -deviation analysis showed that alpine communities were more dissimilar than expected by chance in relation to communities located at lower elevations, which were closer to null expectations (see also Mori et al., 2013). Accordingly, our normalized stochasticity ratio (NST) values decreased substantially above the treeline (Fig. 5). This finding is in agreement with the notion that ecological communities in more benign environments (e.g., those with high productivity) are more likely to be shaped by neutral processes, whereas environmental selection is more plausible in communities thriving in high stress habitats (Chase, 2010; Andrew et al., 2012). Two non-mutually exclusive circumstances may underlie the observed pattern. First, the realized pool of species inhabiting high-elevation environments may be more or less nested within the pool of species that can be found at lower elevations (Chase, 2010). Secondly, habitat specialists seem to be mostly influenced by deterministic factors than generalist species do (e.g., Pandit et al. 2009). Since the proportion of habitat specialists (i.e., taxa with narrow ecological tolerance) increases as environmental conditions become increasingly demanding (Devictor et al., 2010), this may contribute to a larger influence of

deterministic mechanisms (mainly selection) in shaping assemblages at harsh, high-mountain environments. These factors may counterbalance the effect of community size, as it has been recently suggested that ecological drift drives variation in small communities and that they deviate less from null expectations in comparison with larger communities (Siqueira et al., 2019).

Community composition

Bird communities belonging to different habitat types showed distinct spatial separation as illustrated in Fig. 6. Accordingly, the PERMANOVA analysis yielded significant differences among habitats despite the existence of interannual variability in community composition, mostly in alpine environments. When plotting elevation onto the ordination plot, we observed a greater dispersion of the data at an elevation from 2,000 to 2,200 m compared to other elevation levels (inset in Fig. 6). This suggests an above average level of heterogeneity in community composition around the treeline. This heterogeneity probably arises as a result of two factors: spatial variation in the uppermost limit of treeline (Gehrig-Fasel et al., 2007) and the high temporal turnover rate observed at this elevation (as a result of recurrent colonization and extinction events). In addition, during the last decades the proportion of forest area has increased noticeably at high elevations in alpine regions; the higher up, the sharper the relative increase in forest area. For instance, whilst the growth rate at low elevations was minimal during the period 1985-2009, it was 23.1% between elevations of 2,000 and 2,200 m (Swiss Federal Statistical Office SFSO, 2013). Thus, changes in land use probably have contributed to the existence of higher temporal variability in alpine communities.

Imperfect detection

We did not account for imperfect detection of species in our analyses. Although we cannot discard that imperfect detection has influenced our results to some extent, to constitute an important factor behind our findings, species detectability would have needed to change directionally over time and along the elevational gradient, in a way systematically related to our temporal dynamics metrics. In addition, species detectability in this monitoring programme has been assessed and has been proven to

be high (89% according to the Burnham's Jackknife method; see Kéry & Schmid, 2006) in comparison with other programs like the American Breeding Bird survey (Boulinier et al., 1998). In particular, Kéry & Schmid (2006) did not find a significant effect of either elevation or forest cover on detection probability. This result was confirmed in a later study using species-specific occupancy models in which Kéry & Royle (2009) reported that in 97% of cases the estimated number of overlooked species per plot was only 1-4 (proportion of detected species = 91%). On the other hand, metrics are likely to be robust to detection filtering if the effects of the environment on functional diversity and similar estimates are larger than the effects of detection. Regarding this, Johnson (2008) argued that no method of adjusting bird count data appears to be effective for large-scale, multi-species monitoring surveys (i.e., a single method is unlikely to work well across all species). In a more recent review, Banks-Leite et al. (2014) identified several practical limitations associated with the use of detectability models concluding that unadjusted estimates of single- and multiple-species responses to ecological gradients can be just as robust as estimates that were *a posteriori* controlled for covariates of detection probability (see e.g., Welsh et al., 2013). Thus, we think it is unlikely that this issue had a relevant impact on our results.

Conclusions

Most traditional measures of community structure represent a 'snapshot in time' whereas ecological communities are dynamic and many are experiencing directional change over time. Here, we used multivariate methods including recently developed analyses such as the three-term local variance analysis (Lepš et al., 2019) and the NST ratio (Ning et al., 2019) for testing hypotheses of temporal dynamics in Alpine bird communities. Our results provide evidence that niche-based processes are more pronounced in alpine communities, where abiotic conditions are more hostile (and thus, the strength of environmental filtering increases; García-Navas et al., 2020). At lower elevations, the relative contribution of stochastic regulatory mechanisms was greater, yet the assembly of low- and mid-elevation communities was also fundamentally driven by deterministic processes. These findings agree with the idea that, although species turnover in metacommunities is frequent, a high temporal turnover does not necessarily imply the overriding importance of stochastic processes (Freestone &

Inouye, 2015; Leibold & Chase, 2017). According to our results reported here and in a previous study (García-Navas et al., 2020), taxonomic and functional diversity may have a more important role as a stabilizing agent than intraspecific competition (negative covariation) in this Alpine region. Our study shows the convenience of studying community dynamics over long time-periods in order to better understand the mechanisms that shape the identity and abundance of species within natural communities. In particular, this study is one of the first to address the relationship between patterns in community dynamics and elevation, which is of utmost importance from a conservation point of view given the vulnerability of mountain systems to global change impacts (Kohler et al., 2014; Lehikoinen et al., 2019; Perrigo et al., 2019).

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Data accessibility

The data that support the findings of this study are available from the Swiss Ornithological Institute (www.vogelwarte.ch) but restrictions apply to the availability of these data, which were used under license for the current study, and so are not publicly available.

Conflict of interest

The authors declare that they have no conflict of interest.

Biosketch

Vicente García-Navas is a researcher at the Center for Ecology, Evolution and Environmental Changes (cE3c) - University of Lisbon, Portugal. His current project is focused on diversity dynamics in land bird communities. He is interested in how species assemblages change over time and along environmental gradients and the influence of historical processes on local coexistence patterns.

Author contribution

VGN conceived the study; TS and HS provided the dataset; VGN analyzed the data; VGN, TS and AO interpreted the results; VGN wrote the manuscript with inputs from TS and AO.

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Figure captions

Figure 1. Graphical summary of the four main predictions examined in this study (left) and overview of the study area including a representative picture of the four habitat types and a topographic map with the distribution of the 131 plots (right). In brief, the four predictions can be summarized as follows: both temporal turnover (*i*) and synchrony (*ii*) increases with elevation as result of low taxonomic richness, low functional diversity and high ephemerality of populations in high-elevation communities; (*iii*) community stability shows a quadratic relationship with elevation ('hump-shaped' pattern) because the more dynamic habitats (farmlands and alpine environments) tend to be predominant at both extremes of the elevational gradient (at low- [$<1,000$ m] and high- [$>1,800$ m] elevation, respectively); and (*iv*) the relative contribution of stochastic processes increases with elevation due to a stronger effect of environmental filtering as abiotic conditions become harsher and more stressful (see main text for details). (Photo credits: A. Ozgul and T. Sattler).

Figure 2. Plots showing the relationship between elevation and (a) temporal turnover rate, and (b) rate of directional change in bird community composition in the Swiss Alps over the period 1999-2018. Each point corresponds to a different study plot, which is colored according to the habitat type it belongs to (orange: farmland; grey: mixed; green: forest; blue: alpine). Relationships were fitted using polynomial (*turnover rate* elevation: $t = -3.18$, $p < 0.01$; elevation²: $t = 3.68$, $p < 0.001$; elevation³: $t = -3.85$, $p < 0.001$) or linear models (*rate of community change* elevation: $t = -3.50$, $p < 0.001$).

Figure 3. Relationship between community-level species covariance and elevation. Species covariance is shown as log-transformed Schluter' variance ratio (*VR*), which compares the variance of the community as a whole relative to the sum of the individual population variances. All values except two were positive ($VR > 0$), reflecting the rarity of compensatory dynamics (negative covariance). The dotted line indicates the significance threshold. Values above the line are significantly different from that expected by chance (null model).

973

974 *Figure 4.* Variation in the synchrony component due to long-term trends (S_{trend}) and the component
975 due to year-to-year fluctuations ($S_{\text{detrended}}$) along the elevational gradient. Synchrony components were
976 obtained from an overall estimate of community synchrony following the decomposition method
977 proposed by Lepš et al. (2019).

978

979 *Figure 5.* Changes in the relative influence of deterministic *versus* stochastic processes in shaping
980 bird community assembly estimated as (a) Raup-Crick dissimilarity values (β_{RC}), and (b) normalized
981 stochasticity ratio (NST), along an elevational gradient in the Swiss Alps. According to the Raup-
982 Crick' method, a beta-deviation (β_{RC}) close to zero suggests that neutral processes are more important
983 in structuring the community, whereas larger null deviations suggest that niche-based processes are
984 more important (communities are more dissimilar than expected by chance). According to Ning et al.
985 (2019), NST discern between more deterministic (<50%) and more stochastic (>50%) processes being
986 50% the boundary point.

987

988 *Figure 6.* Principal coordinates analysis (PCoA) based on the distance matrix of Bray-Curtis
989 dissimilarity for bird communities (131 study plots, 20 yr). Each dot represents community
990 composition at a site (study plot) for each sample year. Habitat type is indicated by color. The inset
991 shows elevation fitted as a smooth surface onto the ordination plot ('ordisurf' model).

992

Figure 1

Figure 2

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Figure 3

1007 Figure 5

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1009 Figure 6
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1011 *Table 1.* Description of the four habitat categories considered in the present study including
1012 information on mean elevation and mean proportion of surface covered by agriculture land, forests
1013 and alpine environments. Means $\pm$ SD are given (ranges in brackets).

1014
1015

Habitat	<i>n</i>	Elevation (m)	% Farmland	% Forest	% Alpine
Alpine (<i>natural grasslands, alpine meadows, moors, and bare rocks</i>)	44	2063 $\pm$ 325 (1,180-2,710)	2.94 $\pm$ 8.81 (0-36)	9.65 $\pm$ 13.87 (0-45)	84.98 $\pm$ 16.44 (51-100)
Forest (<i>coniferous and broad-leaved/coniferous forests</i>)	46	1445 $\pm$ 365 (590-2,020)	11.92 $\pm$ 12.75 (0-42)	67.77 $\pm$ 12.95 (51-98)	17.18 $\pm$ 14.18 (0-44)
Mixed (<i>forests with significant proportion [$>50\%$] of open habitat</i>)	21	1300 $\pm$ 424 (380-2,030)	27.33 $\pm$ 17.18 (0-50)	40.66 $\pm$ 6.54 (29-50)	24.00 $\pm$ 18.49 (0-49)
Farmland (<i>pastures, non-irrigated arable land, crops-mosaics, and vineyards</i>)	20	949 $\pm$ 394 (390-1,980)	67.95 $\pm$ 12.17 (51-92)	21.04 $\pm$ 14.01 (0-42)	2.27 $\pm$ 4.87 (0-20)

Table 2. Temporal diversity metrics (mean $\pm$ SD) for bird communities in the Swiss Alps estimated over a 20-yr period. Results of ANOVA analyses testing for the existence of habitat differences are given at the bottom.

	Gains	Losses	Turnover rate	Rate of change
Alpine	0.15 $\pm$ 0.04	0.14 $\pm$ 0.04	0.29 $\pm$ 0.07	0.47 $\pm$ 0.54
Forest	0.13 $\pm$ 0.02	0.12 $\pm$ 0.01	0.24 $\pm$ 0.06	0.79 $\pm$ 0.72
Mixed	0.12 $\pm$ 0.01	0.12 $\pm$ 0.01	0.25 $\pm$ 0.04	0.87 $\pm$ 0.58
Farmland	0.12 $\pm$ 0.03	0.11 $\pm$ 0.03	0.24 $\pm$ 0.03	0.66 $\pm$ 0.34
	F _{3,127} = 4.63 p < 0.01	F _{3,127} = 6.78 p < 0.001	F _{3,127} = 8.38 p < 0.001	F _{3,127} = 3.04 p = 0.03

1028 Table 3. Synchrony and community stability metrics (mean $\pm$ SD) for Alpine bird communities
1029 estimated over the period 1999-2018, and results of analyses testing for a linear relationship with
1030 elevation and differences among habitat categories. The average number of species per plot is given in
1031 brackets. Metrics were computed by using both the standard method (a) and the three-term local
1032 variance ($T3$) approach (b) proposed by Lepš et al. (2019) to filter out the pervasive effects of
1033 directional trends on community synchrony (see main text for more details).
1034

	Habitat type				Analyses	
	Alpine (34)	Forest (55)	Mixed (59)	Farmland (57)	Relationship with elevation (*: quadratic term; **: cubic term)	Habitat differences
(a) Standard approach						
ϕ Loreau & de Mazancourt's <i>phi</i>	0.20 $\pm$ 0.12	0.22 $\pm$ 0.14	0.15 $\pm$ 0.11	0.14 $\pm$ 0.08	$t = 1.69$ $p = 0.09$ $t^* = -1.92$ $p = 0.057$ $t^{**} = 2.20$ $p = 0.029$	$F_{3,126} = 2.79$ $p = 0.04$
η Gross et al' <i>eta</i>	0.19 $\pm$ 0.12	0.23 $\pm$ 0.10	0.18 $\pm$ 0.11	0.18 $\pm$ 0.08	$t = 0.59$ $p = 0.56$	$F_{3,126} = 1.54$ $p = 0.21$
η_w Blüthgen et al' weighted <i>eta</i>	0.33 $\pm$ 0.18	0.44 $\pm$ 0.15	0.34 $\pm$ 0.15	0.34 $\pm$ 0.15	$t = -0.05$ $p = 0.96$	$F_{3,126} = 3.76$ $p = 0.01$
Log- transformed Schluter' variance ratio	0.84 $\pm$ 0.47	1.59 $\pm$ 0.48	1.28 $\pm$ 0.48	1.28 $\pm$ 0.48	$t = 3.06$ $p < 0.01$ $t^* = -3.87$ $p < 0.001$	$F_{3,126} = 14.06$ $p < 0.001$
Stability	5.45 $\pm$ 2.17	5.62 $\pm$ 2.17	7.31 $\pm$ 2.87	7.23 $\pm$ 3.19	$t = -3.26$ $p = 0.001$	$F_{3,126} = 4.85$ $p < 0.01$
(b) Three-term local variance ($T3$) approach						
ϕ Loreau & de Mazancourt's <i>phi</i> ($T3$)	0.15 $\pm$ 0.09	0.15 $\pm$ 0.08	0.11 $\pm$ 0.05	0.11 $\pm$ 0.08	$t = 2.38$ $p = 0.02$	$F_{3,126} = 2.37$ $p = 0.07$
η Gross et al' <i>eta</i> ($T3$)	0.12 $\pm$ 0.08	0.17 $\pm$ 0.08	0.13 $\pm$ 0.06	0.13 $\pm$ 0.07	$t = -0.42$ $p = 0.67$	$F_{3,126} = 3.74$ $p = 0.01$
η_w Blüthgen et al' weighted <i>eta</i> ($T3$)	0.26 $\pm$ 0.16	0.35 $\pm$ 0.14	0.28 $\pm$ 0.12	0.28 $\pm$ 0.13	$t = -0.87$ $p = 0.38$	$F_{3,126} = 3.38$ $p = 0.02$
Log- transformed Schluter' variance ratio ($T3$)	2.05 $\pm$ 0.84	4.00 $\pm$ 1.85	3.38 $\pm$ 1.44	3.19 $\pm$ 1.83	$t = 11.21$ $p < 0.001$ $t^* = -4.03$ $p < 0.001$	$F_{3,126} = 13.8$ $p < 0.001$

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Table 4. Results of decomposing overall synchrony estimated for each habitat type into two different components: the component due to long-term trends (S_{trend}) and the effect beyond these trends ($S_{\text{detrended}}$). Values given in brackets denote the percentage of communities with negative values.

	S_{trend}	S_{detrend}
Alpine	0.55 ± 0.12 (23%)	1.07 ± 0.12
Forest	1.71 ± 0.14 (22%)	2.77 ± 0.10
Mixed	1.04 ± 0.11 (43%)	2.35 ± 0.11
Farmland	1.24 ± 0.08 (15%)	1.94 ± 0.08

Spatial heterogeneity in temporal dynamics of Alpine bird communities along an elevational gradient

by Vicente García-Navas, Thomas Sattler, Hans Schmid and Arpat Ozgul

Table S1. Results of ANOVA Type-II Sums of Squares models testing for the effect of elevation and habitat type on different metrics of temporal dynamics for bird communities in the Alps. In those cases in which there was a significant interaction (indicated with double asterisk), we performed Type-III SS models.

	Metric	Elevation	Habitat	Elevation×Habitat
<i>Temporal dynamics</i>	Temporal turnover	$F_{1,122} = 0.17$ $p = 0.67$	$F_{3,122} = 5.00$ $p < 0.01$	$F_{3,122} = 1.45$ $p = 0.23$
	Rate of community change	$F_{1,122} = 7.81$ $p < 0.01$	$F_{3,122} = 1.45$ $p = 0.23$	$F_{3,122} = 1.31$ $p = 0.27$
	Estimated extinction rate	$F_{1,121} = 0.02$ $p = 0.87$	$F_{3,121} = 5.53$ $p < 0.01$	$F_{3,121} = 1.03$ $p = 0.38$
<i>Community synchrony and stability</i>	ϕ Loreau & de Mazancourt's ϕ^{**}	$F_{1,122} = 11.72$ $p < 0.001$	$F_{3,122} = 4.05$ $p < 0.01$	$F_{3,122} = 3.83$ $p = 0.01$
	η Gross et al' η	$F_{1,122} = 0.84$ $p = 0.36$	$F_{3,122} = 1.70$ $p = 0.17$	$F_{3,122} = 1.12$ $p = 0.34$
	η_w Blüthgen et al' weighted η	$F_{1,122} = 0.48$ $p = 0.49$	$F_{3,122} = 3.89$ $p = 0.01$	$F_{3,122} = 0.94$ $p = 0.42$
	Log-transformed Schluter' variance ratio	$F_{1,122} = 0.31$ $p = 0.57$	$F_{3,122} = 9.48$ $p < 0.001$	$F_{3,122} = 2.14$ $p = 0.10$
	Stability	$F_{1,122} = 2.18$ $p = 0.14$	$F_{3,122} = 2.00$ $p = 0.11$	$F_{3,122} = 1.08$ $p = 0.36$
<i>Relative contribution of stochastic vs. deterministic processes</i>	Raup-Crick beta deviation	$F_{1,122} = 0.45$ $p = 0.50$	$F_{3,122} = 4.85$ $p < 0.01$	$F_{1,122} = 0.09$ $p = 0.96$
	NST values ^{**}	$F_{1,121} = 30.98$ $p < 0.001$	$F_{3,121} = 2.61$ $p = 0.05$	$F_{3,121} = 6.06$ $p < 0.001$

Table S2. Correlation matrix showing the relationship between different metrics of synchrony viz. Loreau & de Mazancourt's ϕ (φ), Gross et al' eta (η), Blüthgen et al' weighted eta (η_w), log-transformed Schluter' variance ratio (log VR), the three-term local variance ($T3$) version of each metric, and species richness (SR).

	φ	η	η_w	log VR
φ				
η	0.829***			
η_w	0.835***	0.805***		
log VR	0.530***	0.724***	0.774***	
$T3$	0.616***	0.588***	0.582***	0.667***
SR	-0.358***	-0.129	-0.072	0.418***

Figure S1. Plot showing the relationship between elevation and estimated extinction rates for bird communities in the Swiss Alps over the period 1999-2018. Extinction rates increases sharply between 1,500 and 2,000 and then decreased gain leading to a cubic pattern (*estimated extinction rate* elevation: $t = -3.11, p < 0.01$; elevation²: $t = 3.50, p < 0.001$; elevation³: $t = -3.57, p < 0.001$). Each point corresponds to a different study plot, which is colored according to the habitat type it belongs to (orange: farmland; grey: mixed; green: forest; blue: alpine).

1089 *Figure S2. Relationship between estimated extinction rates for (a) ground-dwelling and (b) arboreal*
 1090 *species, and elevation. The relationship followed a quadratic and cubic pattern, respectively (arboreal*
 1091 *elevation: $t = 2.44, p = 0.016$; ground-dwelling elevation: $t = 2.14, p = 0.03$; elevation²: $t = -1.69, p =$*
 1092 *0.09).*

1094 *Figure S3.* Level of synchrony (ϕ) in species abundances within a community over time estimated
1095 following the Loreau & de Mazancourt's method plotted against elevation. Each point corresponds to
1096 a different study plot, which is colored according to the habitat type it belongs to (orange: farmland;
1097 grey: mixed; green: forest; blue: alpine).
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