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3 **Spatial heterogeneity in temporal dynamics of Alpine bird communities**
4 **along an elevational gradient**
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34 *Abstract* Aim: Mountains are biodiversity hotspots and are among the most sensitive ecosystems to
35 ongoing global change being thus of conservation concern. Under this scenario, assessing how
36 biological communities vary over time along elevational gradients and the relative effects of niche-
37 based deterministic processes and stochastic events in structuring assemblages is essential. Here, we
38 examined how the temporal trends of bird communities vary with elevation over a 20 year-period
39 (1999-2018). We also tested for differences in temporal dynamics among habitat types (among-
40 community variability) and functional groups (within-community variability). Taxon: 97 species of
41 common breeding birds. Location: Swiss Alps. Methods: We used abundance data
42 from the Swiss breeding bird survey to compute different temporal dynamics metrics (temporal
43 turnover, synchrony, rate of community change, and community-level of covariance among species).
44 We also examined the relative contribution of deterministic and stochastic processes in community
45 assembly using the Raup-Crick method and the normalized stochasticity ratio. Results: We found that,
46 with greater elevation, temporal species turnover increased while the rate of overall community
47 change over successive years decreased, suggesting that high-elevation communities display more
48 erratic dynamics with no clear trend. Despite this, we found a more deterministic assembly of alpine
49 communities in comparison to those located at lower elevations. Deterministic processes had greater
50 influence than stochastic processes on community assembly along the entire elevational gradient
51 (80% of communities). Forest communities exhibited higher synchrony in comparison to the
52 remaining habitats likely because they consisted of species with greater functional redundancy,
53 whereas alpine communities were the least stable as a result of their low taxonomic richness
54 ('portfolio' effect). Main conclusions: Community-level synchrony was overall positive supporting
55 the idea that compensatory mechanisms are rare in natural biological communities. Our results
56 suggest that rather than competition, the existence of differences in the ecological strategies of species
57 may have a stabilizing effect on bird communities by weakening the concordance of species responses
58 to fluctuations in environmental conditions (i.e., enhanced interspecific temporal asynchrony). This
59 study provides evidence that, although species turnover in metacommunities is frequent, a high
60 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

88 competition. Regarding this, competition among species is generally expected to increase asynchrony,
89 leading to compensatory dynamics where fluctuations in the density of one species are offset by the
90 opposite fluctuations of (an)other species (González & Loreau, 2009). Therefore, communities with
91 high functional diversity (i.e., those composed of species with different ecological strategies) should
92 be more likely to exhibit a higher level of asynchrony, and thus higher stability than functionally poor
93 assemblages ('portfolio effect': Doak et al. 1998). In addition to community synchrony, several other
94 metrics have been devised in order to quantify how communities change in response to
95 environmental drivers; that is, if they remain invariant, if they gradually track these changes or,
96 instead, they shift abruptly exhibiting early warning signals of ecological collapse (Gaüzère et al.,
97 2015; Blüthgen et al., 2016; Spanbauer et al., 2016). For instance, Collins et al. (2008) employed the
98 rate of compositional change to compare the temporal dynamics of plant species in burned *versus*
99 unburned areas at the Konza Prairie Long-Term Ecological Research (LTER) site.

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

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

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

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

150

151

152 **Material and Methods**

153 *Data collection*

154 We compiled data from the ‘Monitoring Häufige Brutvögel’ (MHB) scheme, a volunteer-based
155 programme aimed at annual monitoring of population dynamics of common breeding species in
156 Switzerland, a small country (41,285 km²) in Western Europe. This programme started in 1999 and
157 follows a standardized territory mapping protocol in which 267 1×1 km plots from a regular grid
158 covering the entire country are surveyed 2-3 times by skilled birdwatchers during the breeding season
159 (15th april-15th June). Observers record every bird seen or heard along a square specific transect route
160 (~5-km long) that does not change over the years (for more details see Schmid et al., 2004; Kéry &
161 Royle, 2009). In this study, we restricted our analysis to the region of the Alps (60% of Switzerland;
162 ~25,000 km²), and selected those plots that have been uninterruptedly surveyed from 1999 to 2018.
163 Observations of the two or three visits were grouped into territories using “TerriMap” (Schmid,
164 2017). Thus, our dataset consisted of relative abundance data (number of territories per site) collected
165 during two decades in 131 plots along a ~2,300 m elevational gradient (range: 380-2,710 m). Study
166 plots were classified into four different habitat categories (forest; farmland; mixed; alpine) according
167 to the predominant land use (see Table 1 and Fig. 1b). Land use information (geostat data at 1×1 km²
168 resolution) was obtained from an aerial survey carried out by the Swiss Federal Office for Statistics
169 (Arealstatistik; www.bfs.admin.ch). Waterbirds, nocturnal birds and raptor species with large home
170 ranges were excluded from the dataset as they are not properly surveyed by the programme. In total,

171 97 common breeding species (accounting for about 99% of the abundance data) were included in the
172 analyses.

173

174 *Quantifying temporal dynamics*

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

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

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

204

205 *Estimating extinction rates*

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

221

222 *Quantifying community stability*

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

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

$$233 \quad \varphi = \frac{\sigma(\chi_T)^2}{(\sum_i \sigma_{\chi_i})^2}$$

234 where:

$$235 \quad \chi_T(t) = \sum_{i=1}^N \chi_i(t)$$

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

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

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

257 Further, we disentangled the effect of directional trends and similarity in year-to-year
258 fluctuations on synchrony indices following two methods recently developed by Lepš and
259 collaborators (2019). The rationale behind this analysis is that long-term directional trends in species
260 composition due to land-use or climate change can lead to an apparent increase in synchrony that is
261 not due to concordant fluctuations in species abundances. To filter out the pervasive effects of
262 directional trends, Lepš et al. have proposed two solutions. The first approach is applicable to the
263 above-mentioned synchrony indices and consists of applying the three-term local variance ($T3$). That
264 is, variance is not computed as the average of squared deviations from the overall mean, but from the
265 squared difference of the middle year (t_0) and average of the year before (t_1) and after (t_{-1}) within a
266 movable 3-yr window (Lepš et al., 2019). The second approach is based on computing synchrony
267 over the residuals of fitted species trends over time. Thereby, it is possible to decompose synchrony
268 into the part that can be ascribed to the directional trend and the part that is due to residual variation
269 (i.e., detrended component) (i.e., $S_{\text{total}} = S_{\text{trend}} + S_{\text{detrended}}$). Thus, for each plot we estimated the $T3$
270 version of each synchrony index (φ , η and η_w) and decomposed total synchrony into two components:
271 the one caused by the trend and the one arising from year-to-year fluctuations.

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

278

279 *Deterministic vs. stochastic processes*

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

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

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

299

300 *Community composition*

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

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

313

314 *Statistical analyses*

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

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

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

334

335

336 **Results**

337

338 *Temporal dynamics*

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

346 The rate of community change decreased with elevation (Fig. 2b). Communities located in
347 mixed habitats displayed the fastest change (i.e., steepest slopes), which suggests that these bird
348 assemblages were increasingly dissimilar over time (Table 2). Meanwhile, alpine environments
349 showed the shallowest time-lag analysis (TLA) slopes, suggesting low directionality in compositional
350 changes of species assemblages inhabiting these environments, in which species appeared and
351 disappeared in a more erratic way. When assessing species exploiting different resources, we found
352 that the arboreal and insectivorous guilds showed steeper TLA slopes ($b = 0.41$ and 0.53 ,
353 respectively) in comparison to the ground-foraging and plant-and-seed-eating guilds, respectively ($b =$
354 0.34 and 0.16).

355

356 *Extinction*

357 The mean value of extinction for all species was $0.19 (\pm 0.05)$, which indicates that on an average
358 survey plot, approximately 19% of species of the original assemblage had become extinct. Estimated
359 extinction rates differed among habitat types (farmland: 0.18 ± 0.05 , mixed: 0.17 ± 0.02 , forest: 0.18
360 ± 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
361 which a sharp decrease was found (see Fig. S1). Extinction rates estimated separately for arboreal

362 species increased positively with elevation, whereas extinction rates of ground-foragers tended to
363 adopt a quadratic pattern (Fig. S2). On the contrary, extinction rates for insectivorous and plant-and-
364 seed-eating guilds did not correlate with elevation (both p -values >0.05). Estimated extinction rates
365 were higher for the herbivorous group (plant, fruit, and seed eaters) in comparison with those obtained
366 for the insectivorous guild (0.34 ± 0.16 vs. 0.18 ± 0.06 ; paired t -test: $t = -10.59$, $p < 0.001$). There were
367 no significant differences in probability of extinction between arboreal and ground-foraging guilds
368 (0.22 ± 0.15 vs. 0.21 ± 0.08 ; $t = -0.62$, $p = 0.53$).

369

370 *Synchrony and community stability metrics*

371 The four synchrony measures used (φ , η , η_w and $\log VR$) were all positively correlated (see Table S2),
372 but only φ was significantly correlated with elevation ($t = 2.23$, $p = 0.03$) probably due to this index
373 being more sensitive to species richness variation than the others (Table S2). However, the
374 polynomial (cubic) model provided a better fit than the linear one (Table 3; Fig. S3). The variance
375 ratio (VR) among species was quadratically related to elevation with maximum values around 1,000-
376 1,500 m (Table 3; Fig. 3). Most plots (87%) exhibited VR values higher than expected by chance and
377 only two presented a negative covariance. All synchrony indices except η differed significantly
378 among habitat types (Table 3). Forest assemblages exhibited the highest values of synchrony and
379 covariance. Alpine, farmland, and mixed habitats showed quite similar values of synchrony, but the
380 variance ratio ($\log VR$) was much lower in alpine environments in comparison to the remaining
381 categories (Table 3). Alpine and forest communities also exhibited the lowest values of stability,
382 which decreased with elevation (Table 3). On the contrary, mixed habitats harbored the most stable
383 communities (Table 3).

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

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

391 When using the three-term local variance ($T3$) approach to filter out the pervasive effects of
392 directional trends on synchrony, we obtained very similar results to those described above; forests
393 harbored the most synchronous communities, although differences between alpine communities and
394 the remaining habitat types were slightly larger (see Table 3). Accordingly, when decomposing
395 synchrony values, we found that habitat differences in synchrony were not governed by differences in
396 directional trends (S_{trend}), which did not differ significantly among habitat categories ($F_{3,126} = 2.51$, $p =$
397 0.062). Habitat differences in species year-to-year fluctuations ($S_{\text{detrended}}$) were significant ($F_{3,126} =$
398 12.17 , $p < 0.001$); forest and alpine communities exhibited the greatest and smallest values of
399 detrended synchrony, respectively (Fig. 4a). $S_{\text{detrended}}$ was quadratically related with elevation (Fig. 4a;
400 elevation: $t = 2.78$, $p < 0.01$, elevation²: $t = -3.52$, $p < 0.001$), whereas S_{trend} showed a less pronounced
401 (non-significant) ‘hump-shaped’ pattern (Fig. 4b). The proportion of communities exhibiting negative
402 S_{trend} values indicative of successional dynamics was much higher (about double) in mixed habitats
403 compared to other categories (Table 4).

404

405 *Deterministic vs. stochastic processes*

406 The Raup-Crick null-based approach allowed us to estimate the magnitude to which beta (β) diversity
407 deviated from the expectation under a random assembly process while taking differences in species
408 richness and relative abundance into account (i.e., beta-deviation, β_{RC}). β_{RC} values adopted a sigmoid
409 curve along the elevational gradient; alpine communities were more dissimilar than expected by
410 chance (i.e., more distant from null expectations) relative to mid-elevation communities, suggesting
411 that changes in β -diversity were not simply due to a random influence of elevation on species in each
412 locality, and instead likely due to elevation acting as an environmental filter (elevation: $t = -2.04$, $p =$
413 0.04 ; elevation²: $t = 2.21$, $p = 0.03$; elevation³: $t = -2.33$, $p = 0.04$; Fig. 5a). Alpine communities had
414 greater β_{RC} values compared to the rest of the habitats (alpine: 0.093 ± 0.04 , forest: 0.064 ± 0.02 ,
415 farmland: 0.066 ± 0.02 , mixed: 0.060 ± 0.02 ; $F_{3,126} = 11.36$, $p < 0.001$).

416 Most communities (80%) showed normalized stochasticity ratio (NST) values <50%
417 indicating the prevalence of deterministic assembly. Alpine communities presented half as large NST
418 values (19.7%) compared to the remaining habitats (forest: 40.5, farmland: 47.2, mixed: 48.3%)
419 ($F_{3,125} = 37.13, p < 0.001$). Accordingly, the relative importance of stochastic processes in governing
420 community diversity decreased with elevation after reaching its maximum around 1,500 m (elevation:
421 $t = 3.19, p < 0.01$; elevation²: $t = -5.45, p < 0.001$; Fig. 5b).

422

423 *Community composition*

424 The PERMANOVA analysis showed significant differences among habitat types ($R^2 = 0.44, F =$
425 $678.01, p = 0.001$) and study year ($R^2 = 0.01, F = 6.35, p = 0.002$), and a habitat \times year interaction
426 ($R^2 = 0.01, F = 2.58, p = 0.015$). Bird communities belonging to different habitat types occupied a
427 different region in the 2-D ordination space (Fig. 6). Almost all the space occupied by communities
428 from mixed habitats overlapped that of forest and farmland assemblages, whereas alpine communities
429 conformed a cluster with the highest level of spatial separation (Fig. 6). When we fitted elevation as
430 environmental vector onto the ordination space, we observed that this factor explained a significant
431 proportion of the variance ($r^2 = 0.81, p = 0.001$). We obtained a similar result when fitting elevation
432 as smoothed surface using a Generalized Additive Model (GAM) ($R^2 = 0.88, t = 429.2, p < 0.001$; see
433 inset in Fig. 6).

434

435

436 **Discussion**

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

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

445

446 *Indices of temporal dynamics and extinction rates*

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

458 The most probable reason for more dynamic communities occurring at high elevation (around
459 1,800-2,000) is that a substantial proportion of species present in these assemblages are close to their
460 physiological limits and their populations are therefore more vulnerable to fluctuations in abiotic
461 conditions, which gives rise to a high temporal turnover (e.g., Sexton et al., 2009; Londoño et al.,
462 2017). Accordingly, we observed that extinction rates increased from 500 to 2,000 m, reinforcing the
463 idea that increasing environmental harshness makes local populations more susceptible to extinction
464 or more prone to move in search of more benign conditions (McCain, 2009). Thus, communities at
465 high elevation are largely made up of species that come and go uninterruptedly as they are at their
466 range boundaries (Sekercioglu et al., 2008). In this sense, there is evidence that some species in the
467 Swiss Alps and other mountain systems are shifting their upper elevational limit in response to the
468 upward advancement of the treeline (e.g., Harsch et al., 2009; Vittoz et al., 2013; Freeman et al.,
469 2018). Nevertheless, although these shifts occur from one year to the next, they take time to
470 consolidate and perpetuate over the years. Above the natural treeline (>2,100 m) only a small subset

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

479 Our time-lag analyses showed that the slope resulting from plotting pairwise temporal
480 dissimilarity values against temporal distances between samples decreased with increasing elevation,
481 suggesting that the way communities change over time varies along an elevational gradient. Time-lag
482 analysis (TLA) revealed an increase in dissimilarity with increasing time lag in lowland communities,
483 mainly those located in mixed habitats (open and successional forests, edge habitats). These transition
484 environments may harbor a considerable number of ‘directional’ species (species that were present
485 earlier, but later become locally extinct or colonizing species that enter the community later and
486 continually increase their abundance). Conversely, alpine communities showed the shallowest slopes,
487 which suggests a more erratic nature (no temporal autocorrelation) of species assemblages in this
488 habitat. The low densities of many alpine species may lead to stochastic disappearances and
489 reappearances. In addition, it may also be due to these assemblages being composed of a mixture of
490 constant species and species that have more erratic or directional species with low temporal variability
491 (Kampichler & van der Jeugd, 2013). Our results agree with those reported by Kampichler et al.
492 (2014) in a comparative analysis of bird communities from a variety of terrestrial ecosystems, from
493 primeval to disturbed forests. They reported that, although the slope, and thus the rate of community
494 change, varied widely among localities (with lowest and highest values for Białowieża’ pristine
495 forests and successional forests, respectively), all assemblages showed significant directional change
496 of community composition (Kampichler et al., 2014). Thus, TLA can yield significant slopes for
497 communities characterized by remarkably different dynamics, and only those communities that are
498 almost entirely composed of species with constant population sizes or those whose species

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

505

506 *Temporal synchrony and community stability*

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

527 environmental fluctuations (e.g., inter-annual climatic fluctuations). Thus, even though most bird
528 species breeding in temperate systems exhibit a similar response to favorable and unfavorable
529 environmental conditions (e.g., most species show higher fitness in warm springs with sufficient
530 precipitation), the level of functional resemblance among species may boost or dampen the influence
531 of environmental filtering on community synchrony (Loreau & de Mazancourt, 2008; Adler et al.
532 2013). Another factor that can either increase or decrease the level of synchrony is the directional
533 change in species composition. For instance, successional changes after some disturbance (e.g., fire or
534 human-induced deforestation) can catalyze community change in a directional way, masking the
535 effect of year-to-year variation (Chapin III et al., 2006; Pandit et al., 2013). When filtering out the
536 effects of directional trends, we observed that the level of synchrony of alpine communities decreased
537 slightly with respect to that of other categories. However, results remained quite similar; the higher
538 synchrony level observed in forest communities cannot be attributed to the existence of habitat-
539 specific long-term directional trends. In fact, when decomposing overall synchrony into trend (S_{trend})
540 and detrended (S_{detrend}) synchrony, we observed that S_{trend} dampens differences in year-to-year
541 variation among habitats.

542 Since community stability and synchrony were negatively correlated, the less stable
543 communities were those located in forests and alpine habitats. On the contrary, farmlands and mixed
544 habitats exhibited the highest community stability values. Our results thus do not support the idea that
545 habitat conversion and historical deforestation result in reduced diversity and asynchrony (*cf.*
546 Blüethgen et al., 2016). It may be due to agriculture in Switzerland being largely dominated by small
547 farms, mostly in the Alps where traditional and agri-environmental practices are more common than
548 in other regions (Jura region and Central Plateau) (BAFU, 2017). Regarding this, theoretical studies
549 have suggested that interspecific competition may stabilize biological communities by enhancing
550 negative covariation in relative abundances of the constituent species (e.g., González & Loreau,
551 2009). However, here we only found two plots with negative covariance values, supporting the view
552 that compensatory dynamics are rare in natural biological communities (Houlahan et al., 2007;
553 Valone & Barber, 2008; but see Hallett et al., 2014). The level of asymmetry between coexisting
554 species seems to constitute a more important factor in terms of community stability. By weakening

555 interspecific temporal synchrony, species functional dissimilarity may have contributed to stabilize
556 communities in farmlands and mixed habitats. Although the alpine communities presented values of
557 synchrony similar to those observed in farmland and mixed-habitat communities, the average level of
558 stability was even lower than that reported for forests. Such a discrepancy probably arises as result of
559 lower taxonomic richness of alpine environments, since temporal stability at the community level
560 cannot be achieved solely by higher asynchrony across species ('insurance effect'; Naeem & Li,
561 1997; Yachi & Loreau, 1999), but also by higher species diversity (the so-called 'portfolio effect';
562 Doak et al., 1998). The negative relationship between community stability and elevation provides
563 support for the notion that species richness acts as a buffer against environmental perturbation, which
564 is highly relevant in conservation terms (Tilman, 1999; García-Palacios et al., 2018; Joseph et al.,
565 2019).

566

567 *Deterministic vs. stochastic processes*

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

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

587

588 *Community composition*

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

603

604 *Imperfect detection*

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

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

625 *Conclusions*

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

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

646

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657

658 *Data accessibility*

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

662

663 *Conflict of interest*

664 The authors declare that they have no conflict of interest.

665

666 *Biosketch*

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

671

672 *Author contribution*

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

675

676 **References**

677

678 Adler, P.B., Fajardo, A., Kleinhesselink, A.R. & Kraft, N.J.B. (2013) Trait-based tests of coexistence
679 mechanisms. *Ecology Letters*, 16, 1294-1306.

680 Alonso, D., Pinyol-Gallemí, A., Alcoverro, T., & Arthur, R. (2015) Fish community reassembly after
681 a coral mass mortality: Higher trophic groups are subject to increased rates of extinction. *Ecology*
682 *Letters*, 18, 451-461.

683 Anderson, M.J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral*
684 *Ecology*, 26: 32-46.

685 Anderson, M.J. (2006) Distance-based tests for homogeneity of multivariate dispersions. *Biometrics*,
686 62, 245-253.

687 Andrew, M.E., Wulder, M.A., Coops, N.C. & Baillargeon, G. (2012) Beta-diversity gradients of
688 butterflies along productivity axes. *Global Ecology and Biogeography*, 21, 352-364.

689 BAFU (2017): Biodiversität in der Schweiz: Zustand und Entwicklung. Ergebnisse des
690 Überwachungssystems im Bereich Biodiversität, Stand 2016. Umwelt-Zustand Nr. 1630.
691 Bundesamt für Umwelt (BAFU), Bern.

692 Banks-Leite, C., Pardini, R., Boscolo, D., Righetto Cassano, C., Püttker, T., Santos Barros, C. &
693 Barlow, J. (2014) Assessing the utility of statistical adjustments for imperfect detection in tropical
694 conservation science. *Journal of Applied Ecology*, 51: 849-859.

695 Beukhof, E., Dencker, T.S., Pecuchet, L., & Lindegren, M. (2019). Spatio-temporal variation in
696 marine fish traits reveals community-wide responses to environmental change. *Marine Ecology*
697 *Progress Series*, 610, 205-222.

698 Blüethgen, N., Simons, N.K., Jung, K., Prati, D., Renner, S.C., Boch, M., et al. (2016) Land use
699 imperils plant and animal community stability through changes in asynchrony rather than
700 diversity. *Nature Communications*, 7, 10697.

701 Boulinier, T., Nichols, J.D., Sauer, J.R., Hines, J.E. & Pollock, K.H. (1998) Estimating species
702 richness: the importance of heterogeneity in species detectability. *Ecology*, 79, 1018-1028.

703 Buckley, H.L., Day, N.J., Case, B.S., Lear, G. & Ellison, A.M. (2018) Multivariate methods for
704 testing hypotheses of temporal community dynamics. *bioRxiv*,
705 doi: <https://doi.org/10.1101/362822>.

706 Burel, F., Aviron, S., Baudry, J., Le Feón, V. & Vasseur, C. (2013) *The Structure and Dynamics of*
707 *Agricultural Landscapes as Drivers of Biodiversity*. In: *Landscape Ecology for Sustainable*
708 *Environment and Culture*. Fu, B. & Jones, B. (Eds.). Chapter 14. Springer.

709 Chapin III, F.S., Robards, M.D., Huntington, H.P., Johnstone, J.F., Trainor, S.F., Kofinas, G.P., Rues,
710 R.W. *et al.* (2006) Directional Changes in Ecological Communities and Social-Ecological
711 Systems: A Framework for Prediction Based on Alaskan Examples. *The American Naturalist*, 168,
712 S36-S49.

713 Chase, J.M. (2010) Stochastic community assembly causes higher biodiversity in more productive
714 environments. *Science*, 328, 1388-1391.

715 Chase, J.M., Kraft, N.J.B., Smith, K.G., Vellend, M. & Inouye, B.D. (2011) Using null models to
716 disentangle variation in community dissimilarity from variation in α -diversity. *Ecosphere*, 2, 24.

717 Cleland, E.E., Collins, S.L., Dickson, T.L., Farrer, E.C., Gross, K.L., Gherardi, L.A. *et al.* (2013)
718 Sensitivity of grassland plant community composition to spatial vs. temporal variation in
719 precipitation. *Ecology*, 94, 1687-1696.

720 Clotfelter, E.D., Pedersen, A.B., Cranford, J.A., Ram, N., Snajdr, E.A., Nolan Jr, V. & Ketterson,
721 E.D. (2007) Acorn mast drives long-term dynamics of rodent and songbird
722 populations. *Oecologia*, 154, 493-503.

723 Collins, S.L. (2000) Disturbance frequency and community stability in native tallgrass prairie.
724 *American Naturalist*, 155, 311-325.

725 Collins, S.L., Micheli, F. & Hartt, L. (2000) A method to determine rates and patterns of variability in
726 ecological communities. *Oikos*, 91, 285-293.

727 Cornwell, W.K. & Ackerly, D. (2009) Community assembly and shifts in the distribution of
728 functional trait values across an environmental gradient in coastal California. *Ecological*
729 *Monographs*, 79, 109-126.

730 Dehling, M.D., Fritz, S.A., Töpfer, T., Päckert, M., Estler, P., Böhning-Gaese, K. & Schleuning, M.
731 (2014) Functional and phylogenetic diversity and assemblage structure of frugivorous birds along
732 an elevational gradient in the tropical Andes. *Ecography*, 37, 1047-1055.

733 Dencker, T.S., Pecuchet, L., Beukhof, E., Richardson, K., Payne, M.R. & Lindegren, M (2017)
734 Temporal and spatial differences between taxonomic and trait biodiversity in a large marine
735 ecosystem: Causes and consequences. *PLoS ONE*, 12, e0189731.

736 Devictor, V. Julliard, R. Clavel, J. Jiguet, F. Lee, A. Couvet, D. (2008) Functional biotic
737 homogenization of bird communities in disturbed landscapes. *Global Ecology and*

738 Biogeography, 17, 252-261.

739 Devictor V., Clavel J., Julliard R., Lavergne S., Mouillot D., Thuiller W., *et al.* (2010). Defining and
740 measuring ecological specialization. *Journal of Applied Ecology*, 47, 15-25.

741 Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O'Malley, R.E. & Thomson, D. (1998) The
742 statistical inevitability of stability-diversity relationships in community ecology. *American*
743 *Naturalist*, 151, 264-276.

744 Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C. *et al.* (2014) Assemblage
745 time series reveal biodiversity change but not systematic loss. *Science*, 344, 296-299.

746 Elton, C.S. (1958) *The ecology of invasions by animals and plants*. Methuen, London, UK.

747 Fox, J., Weisberg, S. (2019) *An R Companion to Applied Regression*, Third edition. Sage, Thousand
748 Oaks CA.

749 Freeman, B.G., Scholer, M.N., Ruiz-Gutierrez, V. & Fitzpatrick, J.W. (2018) Climate change causes
750 upslope shifts and mountaintop extirpations in a tropical bird community. *Proceedings of the*
751 *National Academy of Sciences*, 115, 11982-11987.

752 Freestone, A.L., Inouye, B.D. (2015) Nonrandom community assembly and high temporal turnover
753 promote regional coexistence in tropics but not temperate zone. *Ecology*, 96, 264-273.

754 García-Navas, V., Sattler, T., Schmid, H. & Ozgul, A. (2020) Temporal homogenization of functional
755 and beta diversity in bird communities of the Swiss Alps. *Diversity and Distributions*, 26, 900-
756 911.

757 García-Navas, V., Sattler, T., Schmid, H. & Ozgul, A. High-elevation bird communities in the Swiss
758 Alps exhibit reduced fecundity and lifespan independently of phylogenetic effects. *Submitted*.

759 García-Palacios, P., Gross, N., Gaitán, J. & Maestre, F.T. (2018) Climate mediates the biodiversity–
760 ecosystem stability relationship globally. *Proceedings of the National Academy of Sciences*
761 *USA*, 115, 201800425.

762 Gaüzère, P. Jiguet, F. & Devictor, V. (2015) Rapid adjustment of bird community compositions to
763 local climatic variations and its functional consequences. *Global Change Biology* 21, 3367-3378.

764 Gaüzère, P. Princé, K. & Devictor, V. (2017) Where do they go? The effects of topography and
765 habitat diversity on reducing climatic debt in birds. *Global Change Biology*, 23, 2218-2229.

766 Gross, K., Cardinale, B.J., Fox, J.W., González, A., Loreau, M., Polley, H.W., *et al* (2014) Species
767 richness and the temporal stability of biomass production: a new analysis of recent biodiversity
768 experiments. *American Naturalist*, 183, 1-12.

769 Graham, C.H., Parra, J.L., Rahbek, C., & McGuire, J.A. (2009) Phylogenetic structure in tropical
770 hummingbird communities. *Proceedings of the National Academy of Sciences of the United States*
771 *of America*, 106, 19673-19678.

772 Hallett, L.M., Hsu, J.S., Cleland, E.E., Collins, S.L., Dickson, T.L., Farrer, E.C. *et al.* (2014) Biotic
773 mechanisms of community stability shift along a precipitation gradient. *Ecology*, 95, 1693-1700.

774 Hallett, L.M., Jones, S.K., MacDonald, A.A., Jones, M.B., Flynn, D.F., Ripplinger, J., Slaughter, P.,
775 Gries, C. & Collins, S.L. (2016) *codyn*: An R package of community dynamics metrics. *Methods*
776 *Ecology and Evolution*, 7, 1146-1151.

777 Harms, K.E., Condit, R., Hubbell, S.P. & Foster, R.B. (2001) Habitat associations of trees and shrubs
778 in a 50-ha neotropical forest plot. *Journal of Ecology*, 89, 947-959.

779 Harsch, M.A., Hulme, P.E., McGlone, M.S. & Duncan, R.P. (2009) Are treelines advancing? A global
780 meta-analysis of treeline response to climate warming. *Ecology Letters*, 12, 1040-1049.

781 Hillebrand, H., Blasius, B., Borer, E.T., Chase, J.M., Downing, J.A. *et al.* (2018) Biodiversity change
782 is uncoupled from species richness trends: consequences for conservation and monitoring. *Journal*
783 *of Applied Ecology*, 55, 169-184.

784 Hoover, D.L., Knapp, A.K., & Smith, M.D. (2014) Resistance and resilience of a grassland ecosystem
785 to climate extremes. *Ecology*, 95, 2646-2656.

786 Houlahan, J.E., Currie, D.J., Cottenie, K., Cumming, G.S., Ernest, S.K.M., Findlay, C.S. *et al.* (2007)
787 Compensatory dynamics are rare in natural ecological communities. *Proceedings of the National*
788 *Academy of Sciences of the USA*, 104, 3273-3277.

789 Jarzyna, M.A., Porter, W.F., Maurer, B.A., Zuckerberg, B., & Finley, A.O. (2015) Landscape
790 fragmentation affects responses of avian communities to climate change. *Global Change Biology*,
791 21, 2942-2953.

792 Jarzyna, M.A., Zuckerberg, B., Finley, A.O. & Porter, W.F (2016) Synergistic effects of climate and
793 land cover: grassland birds are more vulnerable to climate change. *Landscape Ecology*, 31, 2275-
794 2290.

795 Jarzyna, M.A. & Jetz, W (2017) A near half-century of temporal change in different facets of avian
796 diversity. *Global Change Biology*, 23, 2999-3011.

797 Jarzyna, M.A., Quintero, I. & Jetz, W (2019) Functional community assembly and turnover along
798 elevation and latitude. *bioRxiv preprint 706523*.

799 Johnson, D.H. (2008) In defense of indices: the case of bird surveys. *Journal of Wildlife Management*,
800 72: 857-868.

801 Jones, S.K., Ripplinger, J. & Collins, S.L. (2017) Species reordering, not changes in richness, drives
802 long-term dynamics in grassland communities. *Ecology Letters*, 20, 1556-1565.

803 Joseph, G.S., Seymour, C.L., Muluvhahotho, M.M., Munyai, T.C., Bishop, T.R. & Foord, S.H. (2019)
804 Stability of Afromontane ant diversity decreases across an elevation gradient. *Global Ecology and*
805 *Conservation*, 17, e00596.

806 Kampichler, C., van Turnhout, C.A.M., Devictor, V. & van der Jeugd, H.P. (2012) Large-scale
807 changes in community composition: determining land use and climate change signals. *PLoS ONE*,
808 7, e35272.

809 Kampichler, C. & van der Jeugd, H.P. (2013) Determining patterns of variability in ecological
810 communities: time lag analysis revisited. *Environmental Ecological Statistics*, 20, 271-284.

811 Kampichler, C., Angeler, D.G., Holmes, R.T., Leito, A., Svensson, S., van der Jeugd, H.P. *et al.*
812 (2014). Temporal dynamics of bird community composition: an analysis of baseline conditions
813 from long-term data. *Oecologia*, 175, 1301-1313.

814 Kaplan, J.O., Krummhardt, K.M. & Zimmermann, N.E. (2009) The prehistoric and preindustrial
815 deforestation of Europe. *Quaternary Science Reviews*, 28, 3016-3034.

816 Kéry, M. & Schmid, H. (2006) Estimating species richness: calibrating a large avian monitoring
817 programme. *Journal of Applied Ecology*, 43: 101-110.

818 Kéry, M. & Royle, J.A. (2009) Inferences about species richness and community structure using
819 species-specific occupancy models in the national Swiss breedingbird survey MHB. In: *Modeling*
820 *Demographic Processes in Marked Populations*. Thomson, D.L., Cooch, E.G., Conroy, M.J.
821 (Eds), pp. 639-656. Springer, New York.

822 Klink, R., Lepš, J., Vermeulen, R. & de Bello, F. (2019) Functional differences stabilize beetle
823 communities by weakening interspecific temporal synchrony. *Ecology*, 100, e02748.

824 Knaus, P., Antoniazza, S., Wechsler, S., Guélat, J., Kéry, M., Strebel, N. & Sattler, T. (2018). *Swiss*
825 *Breeding Bird Atlas 2013–2016. Distribution and population trends of birds in Switzerland and*
826 *Liechtenstein*. Swiss Ornithological Institute, Sempach.

827 Knaus, P., C. Müller, C., Sattler, T., Schmid, H., Strebel, N. & Volet, B. (2019) *The State of Birds in*
828 *Switzerland: Report 2019*. Swiss Ornithological Institute, Sempach.

829 Kolasa, J. & Li, B.L. (2003) Removing the confounding effect of habitat specialization reveals the
830 stabilizing contribution of diversity to species variability. *Proceedings of the Royal Society of*
831 *London B*, 270, 198-201.

832 Kohler, T., Wehrli, A. & Jurek, M. (2014) *Mountains and climate change: A global concern*.
833 Sustainable Mountain Development Series. Bern, Switzerland, Centre for Development and
834 Environment (CDE), Swiss Agency for Development and Cooperation (SDC) and Geographica
835 Bernensia. 136 pp.

836 Kraft, N.J., Adler, P.B., Godoy, O., James, E.C., Fuller, S. & Levine, J.M. (2015) Community
837 assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, 29, 592-599.

838 Legendre, P. & Gauthier, O. (2014) Statistical methods for temporal and space–time analysis of
839 community composition data. *Proceedings of the Royal Society of London B*, 281, 20132728.

840 Lehikoinen, A., Brotons, L., Calladine, J., Campedelli, T., *et al.* (2019). Declining population trends
841 of European mountain birds. *Global Change Biology*, 25, 577-588.

842 Leibold, M.A., Chase, J.M. (2017) *Metacommunity Ecology*. Princeton University Press, Princeton,
843 NJ.

844 Lepš, J., Májeková, M., Vitová, A., Dolezal, J. & de Bello, F. (2018) Stabilizing effects in temporal
845 fluctuations: management, traits and species richness in high-diversity communities. *Ecology*, 99,

846 360-371.

847 Lepš, J., Götzenberger, L., Valencia, E. & de Bello, F. (2019) Accounting for long-term directional
848 trends on year-to-year synchrony in species fluctuations. *Ecography*, *in press*.

849 Li, W. & Stevens, M. (2017) Community temporal variability increases with fluctuating resource
850 availability. *Scientific Reports*, 7, 45280.

851 Londoño, G.A., Chappell, M.A., Jankowski, J.E. and Robinson, S.K. (2017), Do thermoregulatory
852 costs limit altitude distributions of Andean forest birds?. *Functional Ecology*, 31: 204-215.

853 Loreau, M., Naeem, S. & Inchausti, P. (2002) *Biodiversity and ecosystem functioning: synthesis and
854 perspectives*. Oxford University Press, Oxford, UK.

855 Loreau, M. & de Mazancourt, C. (2008) Species synchrony and its drivers: neutral and nonneutral
856 community dynamics in fluctuating environments. *American Naturalist*, 172, 48-66.

857 Loreau, M. & de Mazancourt, C. (2013) Biodiversity and ecosystem stability: a synthesis of
858 underlying mechanisms. *Ecology Letters*, 16, 106-115.

859 Machac, A., Janda, M., Dunn, R.R., & Sanders, N.J. (2011) Elevational gradients in phylogenetic
860 structure of ant communities reveal the interplay of biotic and abiotic constraints on
861 diversity. *Ecography*, 34, 364-371.

862 Maggini, R., Lehmann, A., Kéry, M., Schmid, H., Beniston, M., Jenni, L. & Zbinden, N. (2011) Are
863 Swiss birds tracking climate change? Detecting elevational shifts using response curve shapes.
864 *Ecological Modelling*, 222, 21-32.

865 McCain, C.M. (2009) Global analysis of bird elevational diversity. *Global Ecology and
866 Biogeography*, 18, 346-360.

867 Mori, A.S., Furukawa, T. & Sasaki, T (2013) Response diversity determines the resilience of
868 ecosystems to environmental change. *Biological Reviews*, 88, 349-364.

869 Naeem, S. & Li, S. (1997) Biodiversity enhances ecosystem reliability. *Nature*, 390, 507-509.

870 Ning, D (2019) Normalized Stochasticity Ratio R package.
871 <https://cran.r-project.org/web/packages/NST/NST.pdf>

872 Ning, D., Deng, Y., Tiedje, J.M. & Zhou, J. (2019) A general framework for quantitatively assessing
873 ecological stochasticity. *Proceedings of the National Academy of Science USA*, 116, 16892-
874 16898.

875 Ontiveros, V.J., Capitán, J.A., Arthur, R., Casamayor, E.O., Alonso, D. (2019) Colonization and
876 extinction rates estimated from temporal dynamics of ecological communities: The *island*
877 R package. *Methods in Ecology and Evolution*, 10, 1108-1117.

878 Pandit, S.N., Kolasa, J. & Cottenie, K. (2009) Contrasts between habitat generalists and specialists: an
879 empirical extension to the basic metacommunity framework. *Ecology*, 90, 2253-2262.

880 Pandit, S.N., Kolasa, J. & Cottenie, K. (2013) Population synchrony decreases with richness and
881 increases with environmental fluctuations in an experimental metacommunity. *Oecologia*, 171,
882 237-247.

883 Perrigo, A., Hoorn, C. & Antonelli, A. (2019) Why mountains matter for biodiversity. *Journal of*
884 *Biogeography*, 00, 1-11.

885 Peterson, C.H. (1975) Stability of species and of community for the benthos of two lagoons. *Ecology*,
886 56, 958-965.

887 Raup D. M., Crick R. E. (1979). Measurement of faunal similarity in paleontology. *Journal of*
888 *Paleontology*, 53, 1213-1227.

889 Renner, S.C., Gossner, M.M., Kahl, T., Kalko, E.K.V., Weisser, W.W., Fischer, M., *et al.* (2014)
890 Temporal Changes in Randomness of Bird Communities across Central Europe. *PLoS ONE*, 9,
891 e112347.

892 Roth, T., Allan, E., Pearman, P.B., Amrhein, V. (2018) Functional ecology and imperfect detection of
893 species. *Methods in Ecology and Evolution*, 9, 917-928.

894 Schluter, D. (1984) A Variance Test for Detecting Species Associations, with Some Example
895 Applications. *Ecology*, 65, 998-1005.

896 Schmid, H. (2017) *TerriMap*-online – ein Tool zur rationellen Auswertung von vereinfachten
897 Revierkartierungen. Swiss Ornithological Institute.

898 Schmidt, K.A. & Ostfeld, R.S. (2003) Songbird populations in fluctuating environments: predator
899 responses to pulsed resources. *Ecology*, 84, 406-415.

900 Sekercioglu, C.H., Schneider, S.H., Fay, J.P. & Loarie, S.R. (2008) Climate Change, Elevational
901 Range Shifts, and Bird Extinctions. *Conservation Biology*, 22, 140-150.

902 Sexton, J.P., McIntyre, P.J., Angert, A.L. & Rice, K.J. (2009) Evolution and Ecology of Species
903 Range Limits. *Annual Review of Ecology, Evolution, and Systematics*, 40, 415-436.

904 Siqueira, T., Saito, V.S., Bini, L.M., Melo, A.S., Petsch, D.K., Landeiro, V.L. *et al.* (2019)
905 Community size affects the signals of ecological drift and niche selection on biodiversity.
906 *BioRxiv* 515098; doi: <https://doi.org/10.1101/515098>.

907 Spanbauer, T.L., Allen, C.R., Angeler, D.G., Eason, T., Fritz, S.C., Garmestani, A.S. *et al.* (2016).
908 Body size distributions signal a regime shift in a lake ecosystem. *Proceedings of the Royal Society*
909 *of London B*, 283, 20160249.

910 Spotswood, E.N., Bartolome, J.W., Allen-Diaz, B. (2015) Hotspots of Community Change: Temporal
911 Dynamics Are Spatially Variable in Understory Plant Composition of a California Oak Woodland.
912 *PLoS ONE*, 10, e0133501.

913 Storchová, L., Hořák, D. (2018) Life-history characteristics of European birds. *Global Ecology and*
914 *Biogeography*, 27: 400-406.

915 Gonzalez, A. & Loreau, M. (2009) The Causes and Consequences of Compensatory Dynamics in
916 Ecological Communities. *Annual Review Ecology, Evolution and Systematics*, 40, 393-414.

917 Supp, S.R. & Ernest, S.K. (2014) Species-level and community-level responses to disturbance: a
918 cross-community analysis. *Ecology*, 95, 1717-1723.

919 Schmid, H., Zbinden, N., Keller, V., (2004) *Überwachung der Bestandsentwicklung häufiger*
920 *Brutvögel in der Schweiz*. Schweizerische Vogelwarte, Sempach.

921 Swiss Federal Statistical Office (2013) *Land use in Switzerland. Results of the Swiss land use*
922 *statistics*. Swiss Statistics series, Neuchâtel. <<http://landuse-stat.admin.ch>>

923 Tilman, D. (1999) The ecological consequences of changes in biodiversity: a search for general
924 principles. *Ecology*, 80, 1455-1474.

925 Tilman, D., Reich, P.B. & Knops, J.M.H. (2006) Biodiversity and ecosystem stability in a decade-
926 long grassland experiment. *Nature*, 441, 629-632.

927 Travis, J.M.J., Brooker, R.W., Clark, E.J. & Dytham, C. (2006) The distribution of positive and
928 negative species interactions across environmental gradients on a dual-lattice model. *Journal of*
929 *Theoretical Biology*, 241, 896-902.

930 Valone, T.J. & Barber, N.A. (2008) An empirical evaluation of the insurance hypothesis in diversity-
931 stability models. *Ecology*, 89, 522-531.

932 Vellend, M. (2016) *The Theory of Ecological Communities*. Princeton University Press. 248 pp.

933 Vittoz, P., Cherix, D., Gonseth, Y., Lubinid, V., Maggini, R., Zbindenf, N. & Zumbachg, S. (2013)
934 Climate change impacts on biodiversity in Switzerland: A review. *Journal for Nature*
935 *Conservation*, 21, 154-162.

936 Welsh, A.H., Lindenmayer, D.B. & Donnelly, C.F. (2013) Fitting and Interpreting Occupancy
937 Models. *PLoS ONE*, 8: e52015.

938 Yachi, S. & Loreau, M. (1999) Biodiversity and ecosystem productivity in a fluctuating environment:
939 The insurance hypothesis. *Proceedings of the National Academy of Sciences USA*, 96, 1463-1468.

940 Zamora, R., Pérez-Luque, A.J. & Bonet, F.J. (2017) *Monitoring global change in high mountains*. In:
941 *High Mountain Conservation in a Changing World*. Catalan, J., Ninot, J.M. & Aniz, M. (Eds.) pp
942 385-413. Springer-Verlag.

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945

946 *Figure captions*

947

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

959

960 *Figure 2.* Plots showing the relationship between elevation and (a) temporal turnover rate, and (b) rate
961 of directional change in bird community composition in the Swiss Alps over the period 1999-2018.
962 Each point corresponds to a different study plot, which is colored according to the habitat type it
963 belongs to (orange: farmland; grey: mixed; green: forest; blue: alpine). Relationships were fitted using
964 polynomial (*turnover rate* elevation: $t = -3.18, p < 0.01$; elevation²: $t = 3.68, p < 0.001$; elevation³: $t = -$
965 $3.85, p < 0.001$) or linear models (*rate of community change* elevation: $t = -3.50, p < 0.001$).

966

967 *Figure 3.* Relationship between community-level species covariance and elevation. Species
968 covariance is shown as log-transformed Schluter' variance ratio (*VR*), which compares the variance of
969 the community as a whole relative to the sum of the individual population variances. All values
970 except two were positive ($VR > 0$), reflecting the rarity of compensatory dynamics (negative
971 covariance). The dotted line indicates the significance threshold. Values above the line are
972 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).

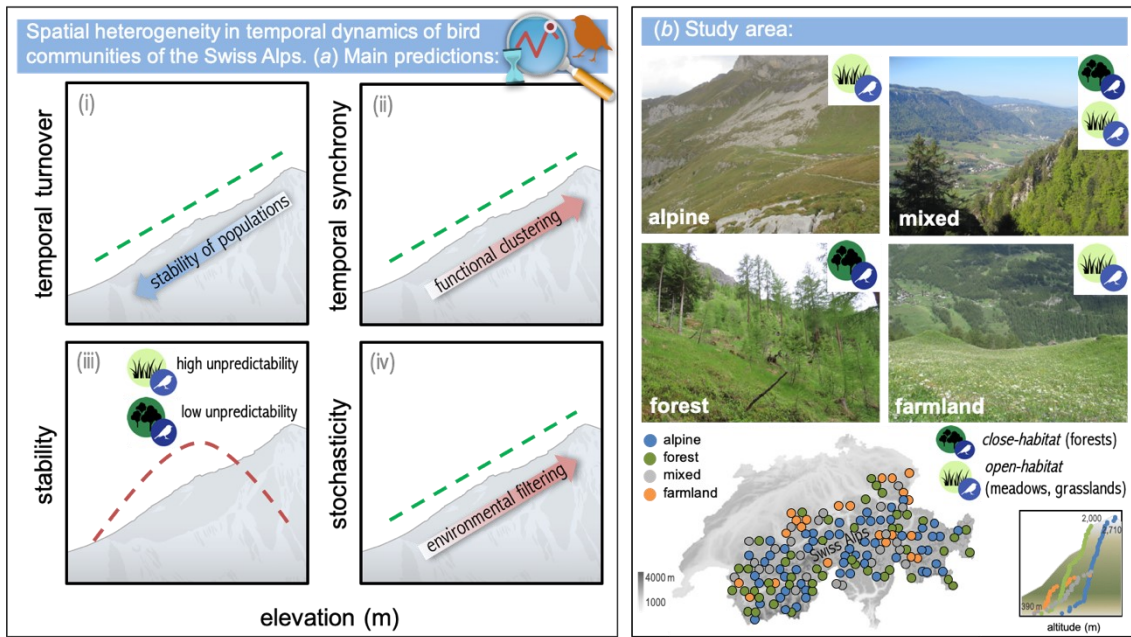
978

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).

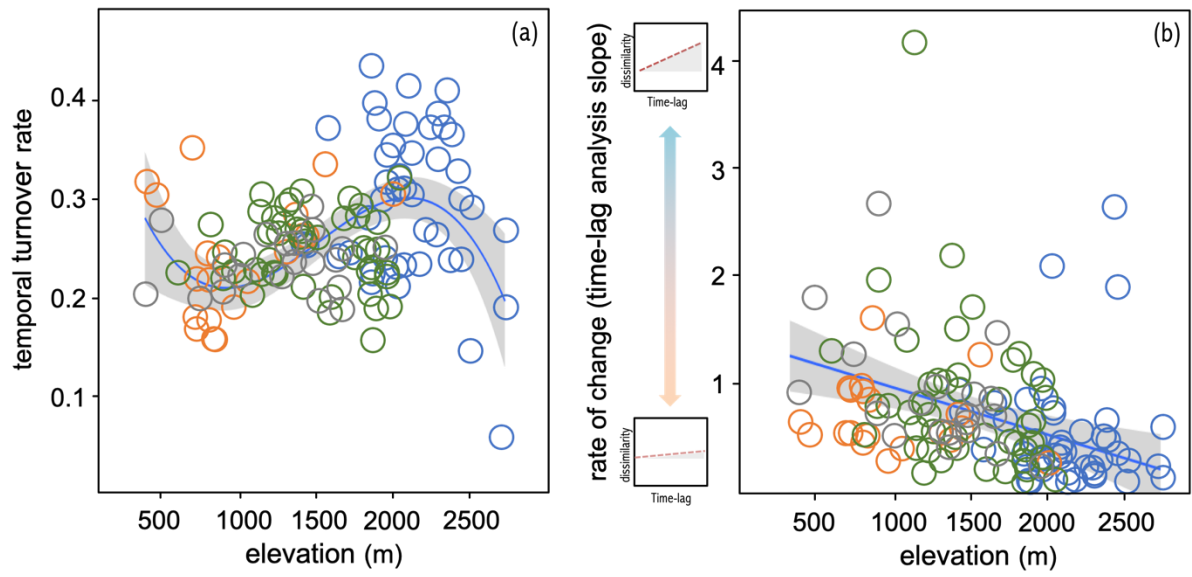
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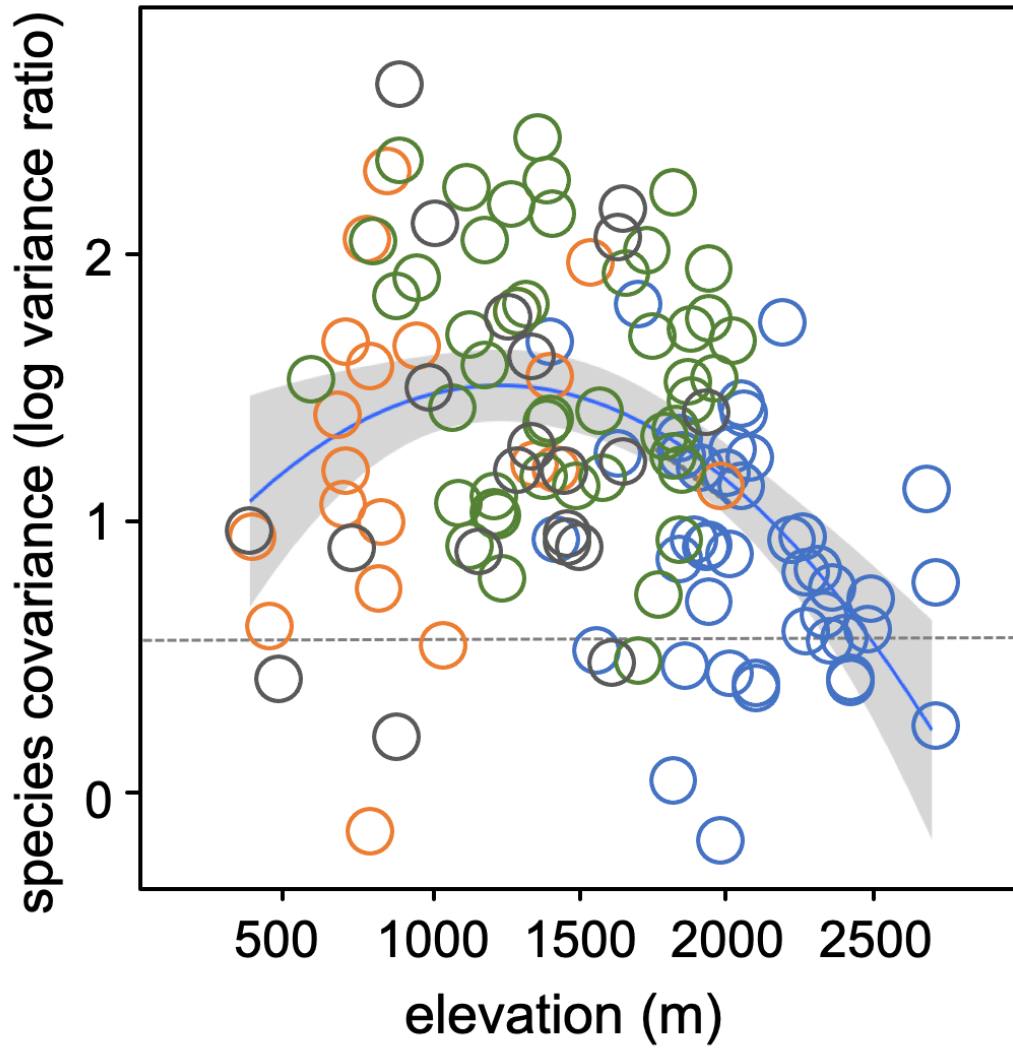


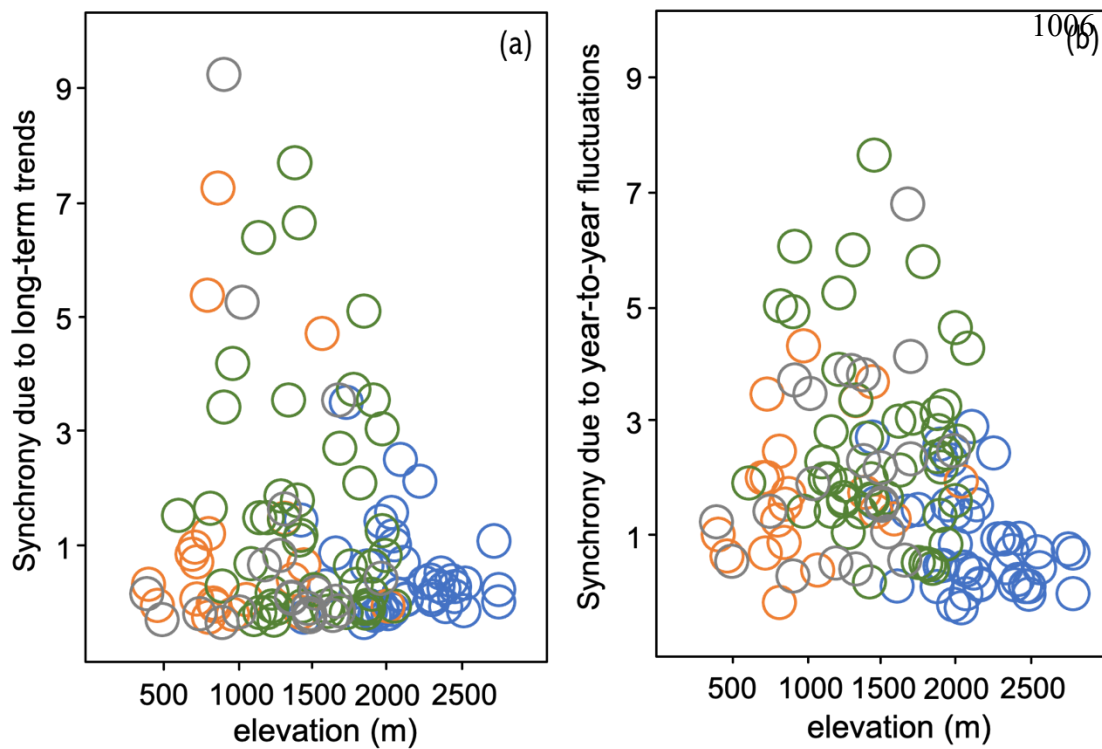
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1003 Figure 3

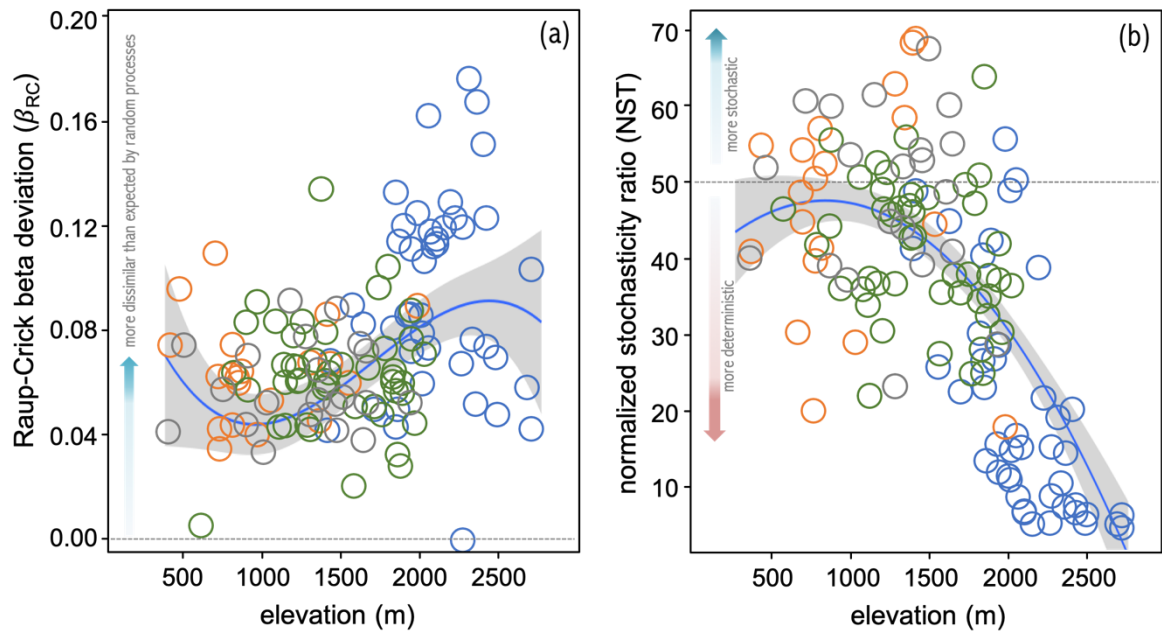
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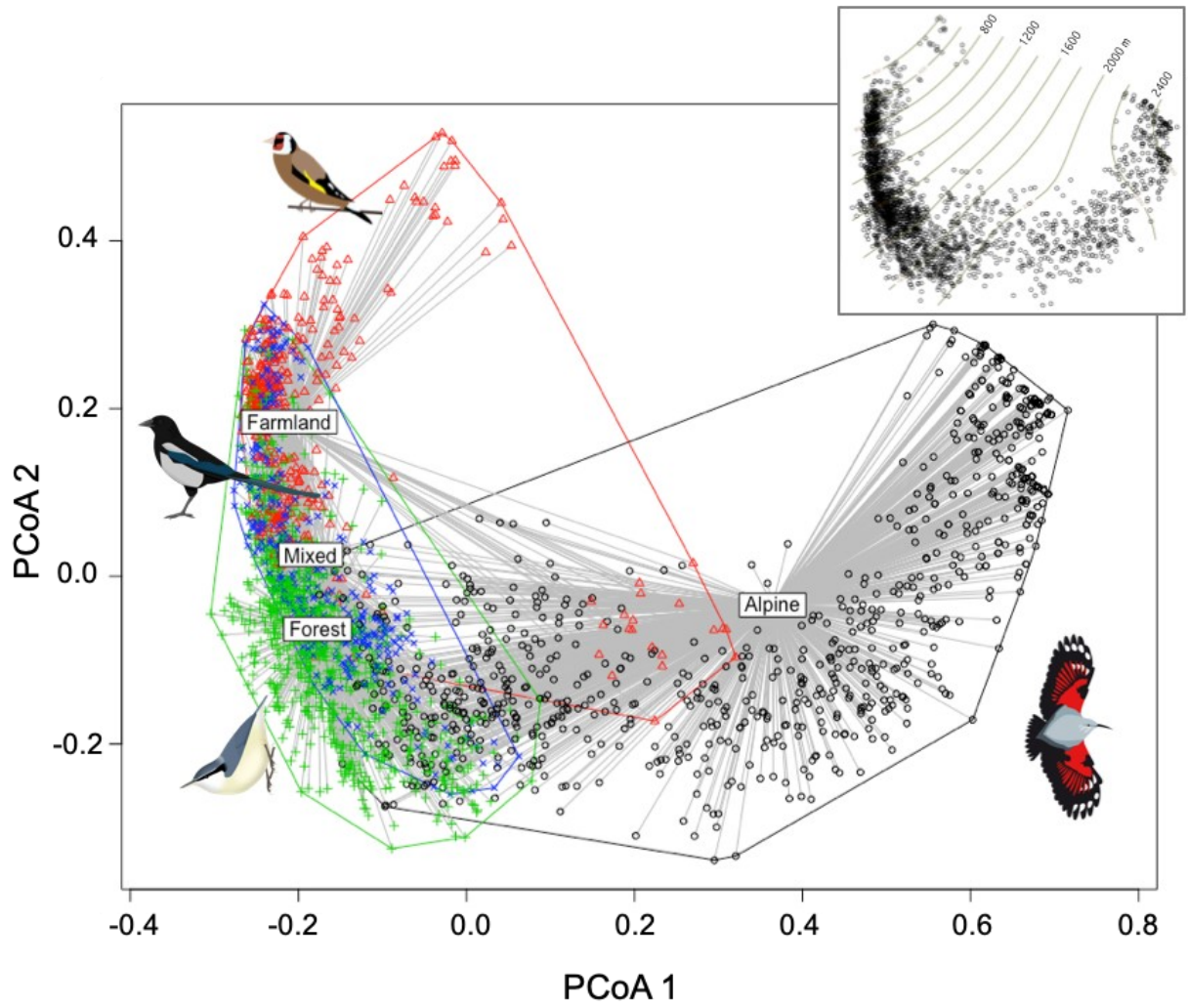
1007 Figure 5

1008



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)

1016 *Table 2.* Temporal diversity metrics (mean \pm SD) for bird communities in the Swiss Alps estimated
 1017 over a 20-yr period. Results of ANOVA analyses testing for the existence of habitat differences are
 1018 given at the bottom.

1019

1020

1021

	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)	<i>Relationship with elevation</i> (*: quadratic term; ** : cubic term)	<i>Habitat differences</i>
(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 (<i>T3</i>) approach						
φ Loreau & de Mazancourt's <i>phi (T3)</i>	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> <i>(T3)</i>	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> <i>(T3)</i>	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 <i>(T3)</i>	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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1037 Table 4. Results of decomposing overall synchrony estimated for each habitat type into two different
1038 components: the component due to long-term trends (S_{trend}) and the effect beyond these trends
1039 ($S_{\text{detrended}}$). Values given in brackets denote the percentage of communities with negative values.
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	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

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SUPPLEMENTARY MATERIAL FOR

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

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

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Table S1. Results of ANOVA Type-II Sums of Squares models testing for the effect of elevation and

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habitat type on different metrics of temporal dynamics for bird communities in the Alps. In those

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cases in which there was a significant interaction (indicated with double asterisk), we performed

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Type-III SS models.

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	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**	$F_{1,121} = 30.98$ $p < 0.001$	$F_{3,121} = 2.61$ $p = 0.05$	$F_{3,121} = 6.06$ $p < 0.001$

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1058 *Table S2.* Correlation matrix showing the relationship between different metrics of synchrony *viz.*
 1059 Loreau & de Mazancourt's *phi* (φ), Gross et al' eta (η), Blüthgen et al' weighted eta (η_w), log-
 1060 transformed Schluter' variance ratio ($\log VR$), the three-term local variance (*T3*) version of each
 1061 metric, and species richness (SR).

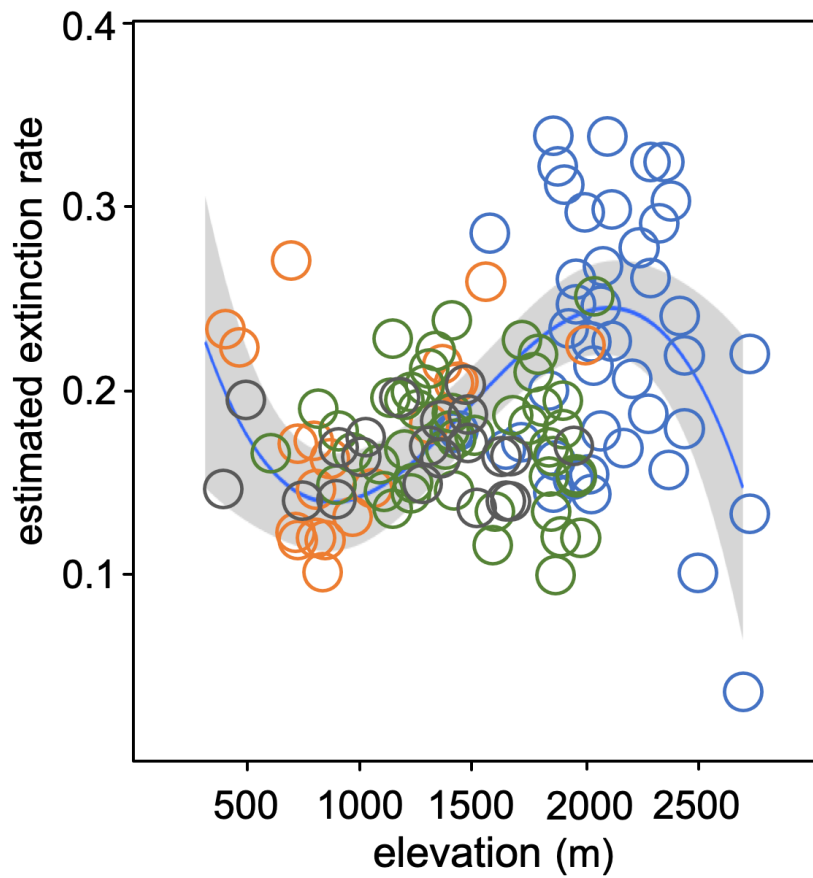
	φ	η	η_w	$\log VR$
φ				
η	0.829***			
η_w	0.835***	0.805***		
$\log VR$	0.530***	0.724***	0.774***	
<i>T3</i>	0.616***	0.588***	0.582***	0.667***
SR	-0.358***	-0.129	-0.072	0.418***

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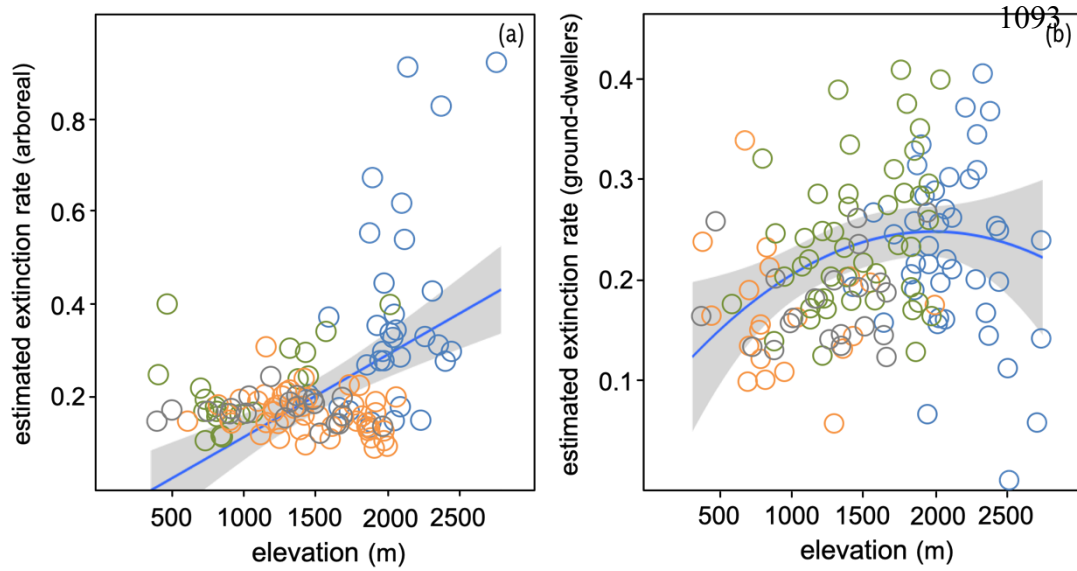
1081 *Figure S1*. Plot showing the relationship between elevation and estimated extinction rates for bird
1082 communities in the Swiss Alps over the period 1999-2018. Extinction rates increases sharply between
1083 1,500 and 2,000 and then decreased gain leading to a cubic pattern (*estimated extinction rate*
1084 *elevation*: $t = -3.11, p < 0.01$; *elevation*²: $t = 3.50, p < 0.001$; *elevation*³: $t = -3.57, p < 0.001$). Each
1085 point corresponds to a different study plot, which is colored according to the habitat type it belongs to
1086 (orange: farmland; grey: mixed; green: forest; blue: alpine).

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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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