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High elevation bird communities in the Swiss Alps exhibit reduced fecundity and lifespan independently of phylogenetic effects

García-Navas, Vicente ; Sattler, Thomas ; Schmid, Hans ; Ozgul, Arpat

Abstract: The merging of community ecology and phylogenetic biology allows us to link broader evolutionary processes to local ecological processes, thereby increasing our understanding of community assembly. A recurrent way to test how species assemblages respond to different abiotic conditions and evaluate the role of evolutionary constraints in community assembly is through using environmental gradients as natural treatments. Here, we combine phylogenetic and trait-based methods to evaluate how the phylogenetic diversity and composition of bird assemblages and their community-weighted traits vary along an elevational gradient in the Swiss Alps. For this purpose, we used four life-history traits considered to be key indicators of individual species response to environmental changes: clutch size, number of breeding attempts, dispersal capacity and lifespan. Controlling for phylogeny, we determined whether environmental filters (elevation, habitat type) act on these traits independently of the level of relatedness among species. We found that phylogenetic dispersion decreases with elevation, but the signature of phylogenetic clustering was weak. Phylogenetic fuzzy weighting showed that the distribution of bird species across plots was related to the two environmental gradients; nonetheless, such influence was not determined by the phylogenetic relationships in either case. That is, there are no specific clades associated with particular elevation or habitat types. We also found that high elevation communities around the treeline were composed of species with lower reproductive rates, reduced lifespan, and lower dispersal capacity, which would make them less resilient to environmental change. Although traits showed moderate phylogenetic signal, only the lifespan was phylogenetically structured. In the remaining cases, the trait-environment association was not mediated by the phylogenetic relationships among taxa. Our study indicates that evolutionary constraints do not represent a significant driver of community assembly in Alpine bird communities and support the notion that phylogeny may often not be a good proxy for traits subject to environmental filtering.

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High elevation bird communities in the Swiss Alps exhibit reduced fecundity and lifespan independently of phylogenetic effects

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31

32 *Abstract*

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60

Introduction

Understanding what drives variation in species diversity and composition across local communities has challenged ecologists for more than a century (Ricklefs, 2004). With the advent of phylogenetic tools 20 years ago, it has been feasible to use patterns of phylogenetic distance or dispersion among members in a community to infer the nature and strength of the eco-evolutionary processes that shape community assembly (Webb et al., 2002; Kembel, 2009). This emerging field, community phylogenetics, incorporates perspectives on clade-level evolution into classic studies of community assembly and has prompted a large body of research over the last decades (Cadotte and Davies, 2016). Based on this, it is widely accepted that assembly represents the outcome of differing strengths of two opposing forces: environmental filtering that increases species similarity through abiotic constraints (Cornwell et al., 2006), and competitive interactions that limit the level of ecological similarity among co-occurring species (Cavender-Bares et al., 2004). The two processes result in contrasting predictions about the phylogenetic relatedness of species that make up the communities. Under environmental filtering conditions, biological communities tend to exhibit lower phylogenetic diversity than expected based on a random sample from the regional pool ('phylogenetic clustering'), as only a few lineages of closely-related species with similar, conserved characteristics can persist (Kraft and Ackerly, 2010; Lebrija-Trejos et al., 2010). In contrast, intraspecific competition and associated mechanisms like niche differentiation and limiting similarity favor the existence of higher phylogenetic diversity than expected by chance ('phylogenetic overdispersion'; e.g. Machac et al., 2011). As opposed to these niche-based predictions, neutrality-based theories emphasize the role of stochastic events, such as local extinction, in structuring species assemblages, giving rise to random fluctuations of species composition among local

communities (i.e., neutral model; Hubbell, 2001). These processes are not mutually exclusive; deterministic and stochastic processes coexist. Although their relative contribution to community assembly usually varies depending on environmental context, the prevalence of deterministic processes being higher in harsher/more stressful environments (Chase, 2007; Chase and Myers, 2011). Regarding this latter, most evidence comes from studies carried out in systems characterized by a progressive spatial change in environmental factors across the space (e.g. Hoiss et al., 2012; Spasojevic and Sudding, 2012; Pellisier et al., 2013). Environmental gradients, therefore, constitute ideal scenarios to examine the role that different processes play in structuring biological communities under different abiotic conditions.

Mountains provide steep clines in climatic and environmental conditions over relatively short distances which makes them excellent natural laboratories to explore how the functional and phylogenetic properties of species assemblages respond to environmental change (Körner, 2000, 2007; Malhi et al., 2010). Although a plethora of studies on plants have investigated changes in phylogenetic structuring along elevational gradients (e.g. Swenson and Enquist, 2009; Qian et al., 2014; Kessler et al., 2016; Luo et al., 2019), studies on vertebrate communities are much scarcer, especially in temperate mountain ranges. A recurrent finding in previous studies from tropical latitudes is the existence of phylogenetic clustering at high elevation (Graham et al., 2009; Cisneros et al., 2014; Hanz et al., 2019), a pattern that may not be pervasive at northern latitudes (Montaño-Centellas et al., 2020). Phylogenetic diversity provides clues on the mechanisms underlying the assembly of communities and reflects the evolutionary history of species within them. For instance, mountain tops have been suggested to represent refugia where we might expect to find ancient or relict lineages (Lomolino, 2001; Perrigo et al., 2019). Following this reasoning, montane communities

should harbor a lower number of clades but, in turn, a higher number of phylogenetically distinct taxa (i.e., species with few close relatives) (Faith, 2016).

Species inhabiting alpine environments may also exhibit distinctive functional traits, which determine their response to pressures and drivers of change (Violle et al., 2007; de Bello et al., 2010). Responses of organisms to environmental stressors at high elevation include behavioural and physiological adaptations like increased breathing rate and higher resting metabolism, as well as life-history syndromes that fall into the ‘slow’ part (e.g. low reproductive rates) of the fast-slow continuum. Scaling up to the community level, these different adaptations and survival strategies exhibited by the different species conforming an assemblage can be summarized into a single value through community weighted mean trait values (i.e., trait values weighted by the relative abundance of each species), which reflect the locally optimal (dominant) trait strategy of the community as a whole (Muscarella and Uriarte, 2016). Community weighted means of traits (CWM) are closely linked to the selection effect and constitute a direct measure of the functional identity of a species assemblage (Roscher et al., 2012). This approach has become quite popular in plant ecology fueling a large body of literature on the relationship between traits linked to the Leaf (or Wood) Economics spectrum and environmental factors (e.g. Hulshof et al., 2013; Fortunel et al., 2014; Schellenberger Costa et al., 2017; Roos et al., 2019), and the development of online trait databases (Kleyer et al., 2008; Kattge et al., 2011). However, relatively few studies have addressed how CWM of traits describing the fast-slow continuum vary along specific environmental gradients in communities of higher trophic levels (but see e.g. Vandewalle et al., 2010, Luck et al., 2012). On the other hand, the existence of a trait-environment relationship may not be exclusively linked to ecological processes, but may also reflect the evolutionary legacy shared by co-occurring species. It happens

when both life-history traits and species composition across communities are phylogenetically structured (Duarte et al., 2018). Hence, in some circumstances, trait conservatism may constrain the types of habitat that can be occupied by some lineages in relation to all habitats available in the landscape ('phylogenetic habitat filtering' *sensu* Duarte 2011). By integrating the evolutionary history of species with life-history traits, it is possible to make stronger inferences regarding community assembly and, for instance, discern between environmental filtering and trait-based convergence. Consequently, there is growing awareness that the combination of these two aspects constitutes a promising and more than timely avenue of research (Pillar and Duarte 2010; Pavoine et al. 2011; Cadotte et al., 2013).

In this study, we examined the associations among environment, life-history traits, and evolutionary history in bird communities of the Swiss Alps, and studied how the phylogenetic diversity, structure and composition of communities vary along an elevational gradient and among habitat types. In a second step, we tested whether these environmental filters act on species traits (clutch size, number of breeding attempts, dispersal capacity and lifespan) independent of the phylogeny. That is, whether elevation and/or habitat influences the mean values of each trait across assemblages after controlling for phylogenetic relationships among species. Specifically, we aimed at elucidating the following questions: (i) How do high *vs.* low elevation communities differ in phylogenetic diversity or number of phylogenetically distinct taxa? (ii) How are the productivity and persistence (i.e., ephemerality) of communities affected by elevation? (iii) How does species composition change relative to habitat and elevation? (iv) To what extent are such trait-environment relationships constrained by phylogenetic relationships among species? We expected that the effect of habitat type and elevation could lead to differences in species distribution, and consequently in phylogenetic and

functional structuring of bird assemblages. Hence, our hypotheses are that the environmental gradient affects CWM across local communities, and that the distribution of species depends on trait similarity among communities.

Material and Methods

Bird assemblages

Bird abundance data were obtained from the Swiss common breeding bird monitoring program ('Monitoring Häufige Brutvögel', MHB), launched and coordinated by the Swiss Ornithological Institute, and which consists of a grid of 1×1 km squares (plots) across Switzerland. This long-term monitoring scheme has been carried out systematically since 1999 in the same plots following a territory mapping protocol (Kéry and Schmid, 2006). In brief, each plot was surveyed by the same observer 2-3 times a year during the breeding season (15th April-15th July) by counting all birds detected visually or acoustically along a transect route. We restricted our study to the Alps, which comprises 151 plots scattered across this biogeographical region over a variety of environments and land-use types. For the purposes of the present study, and following the methodology employed previously (García-Navas et al., 2020), waterbirds, nocturnal birds and raptor species with large home ranges were discarded from the analysis as they are not efficiently captured by this monitoring scheme. We also excluded rare species whose presence in a given plot was not maintained over time and was considered anecdotal. This left 96 common species available for the analysis.

Analyses were based on eight years of data distributed over the time-series (namely, seasons 1999, 2003, 2005, 2008, 2011, 2013, 2015, and 2018) in order to account for interannual variability in bird abundance and obtain robust estimates for

each of the different metrics employed here (see more below). We did not consider the full dataset as we were not interested in the temporal variation of these metrics.

Environmental variables

For each 1×1 km study plot, we obtained information on mean elevation (meters a.s.l.; the mean value from 100 points, one per hectare) and predominant habitat type (three categories: “farmland”, “forest”, and “alpine”) according to land use information provided by the Swiss Federal Statistics Office (www.bfs.admin.ch). We then computed a pairwise dissimilarity matrix for both variables (elevation and habitat) in order to examine trait variation along both environmental gradients through phylogenetic fuzzy weighting analyses (see more below). The habitat dissimilarity matrix was obtained from the proportion of each habitat category represented in each of the plots. The proportion of farmland habitat tended to decrease with elevation, this habitat being almost non-existent above 2,000 meters. The percentage of forest habitat showed a ‘hump-shape’ pattern reaching their maximum values around 1,250-1,750 m. The proportion of alpine habitat increased with elevation, this habitat being almost residual below 1,200 m and accounting for the entire surface above 1,800 m. In most cases, the proportion of habitat in which each plot was classified was higher than 50% (e.g. only those habitats with % of alpine habitat >50 were considered as alpine). Hence, the average proportion of alpine (*a*), forest (*b*) and farmland (*c*) habitat for each habitat category was as follows: alpine habitat; *a*: 80.4%, *b*: 12.9%, *c*: 3.9%; forest habitat; *a*: 18.3%, *b*: 64.0%, *c*: 13.6%; farmland habitat; *a*: 3.5%, *b*: 26.0%, *c*: 62.0%. It must be noted that the Swiss Alps are characterized by patchy and highly heterogenous landscapes; there are no large forested areas in this region (authors, *pers. obs.*).

Functional traits and phylogenetic relationships

Bird species were characterized in relation to four key life-history traits (clutch size, number of breeding attempts, dispersal capacity, and lifespan) most of which have been shown to vary with elevation (see e.g. Boyle et al., 2016; Hille and Cooper, 2015) and that largely define the evolutionary strategies (*r-K* continuum) and the turnover rate of communities. We used maximum longevity as our measure of lifespan as it is the best available estimator and because of the amount of high-quality longevity data available (Healy et al., 2014). Information on traits for each species was compiled from the literature (European Bird Trait Database; Storchová and Hořák, 2018) and a trait database provided by the Bird Migration Department of the Swiss Ornithological Institute (<https://www.vogelwarte.ch/en/projects/bird-migration/>). Dispersal capacity was estimated from the relationship between body size (mass) and wing size (see e.g. Guetté et al. 2017). Higher values indicate species have a larger wing to mass ratio and thus a higher dispersal capacity (e.g. common swift *Apus apus*).

Ultrametric phylogenetic distances between the 96 species were retrieved from a Maximum Clade Credibility (MCC) tree (i.e., the tree that has the maximum product of posterior clade probabilities) obtained from a sample of 100 maximum-likelihood trees assembled by Thuiller et al. (2011) using the R package *phangorn* (Schliep, 2011). The MCC method assumes that the sampled, fully resolved topology with the highest clade credibility is an adequate summary of the most probable clades, with parameter estimates from compatible sampled trees used to obtain the marginal distributions of parameters such as clade ages and branch lengths.

Community-weighted means

For each plot ($n = 151$), the mean species trait values were weighted by using community-weighted means (CWM). A community weighted mean is the average of the local distribution of a trait in a community (Lavorel et al., 2008) and is computed as follows:

$$CWM_t = \sum_{i=1}^n p_i x_i$$

where CWM_t is the community-weighted mean value of a given trait (t), p_i is the relative abundance of the species i , x_i is the mean trait value of species i , and n is the number of species. CWM enables one to examine the association between trait dominance and an environmental gradient for a set of local communities. We computed CWM for each trait -clutch size (CS), number of breeding attempts (NB), dispersal capacity (DIS), and lifespan (LS)- and these were subsequently used to examine the differences in species composition along an environmental gradient. As the relationship between the response variable and elevation was non-linear in some cases, we fitted polynomial models. We chose the most likely model (i.e., the degree with the best performance) based on both model complexity and data fit using the Akaike Information Criterion.

Phylogenetic diversity, structure and composition of communities

In order to examine changes in bird communities in terms of phylogenetic diversity we used the Evolutionary Distinctiveness (ED) score, which approximates the evolutionary history that each species embodies and sums to the phylogenetic diversity of the entire tree (Redding and Moers, 2006; Isaac et al., 2007). This metric has been employed to estimate how much evolutionary distinctiveness would be lost if a given taxon becomes extinct and to guide conservation actions (the EDGE of existence program; Zoological Society of London, 2008) We obtained the ED score for each species and subsequently

computed the community evolutionary distinctiveness (CED) as the community-weighted mean considering all species co-occurring in a given plot. In this way, we tested whether certain elevations or habitats harbor communities that represent a larger amount of evolutionary information compared to others.

Next, we analyzed how the phylogenetic structure of communities varies along the environmental gradient using the standardized Mean pairwise Phylogenetic Distance (MPD). The MPD is the mean phylogenetic distance between all pairs of species in a plot and summarizes the distance between all species combinations in a community, which is independent of species richness (Swenson, 2014). Standardized effect sizes (SES) describe the difference between phylogenetic distances in the observed communities *versus* null communities generated using randomization method, divided by the standard deviation of phylogenetic distances in the null data. SES were computed using the ‘ses.mpd’ function in the R package *picante* (Kembel et al., 2010) assuming an ‘independent swap’ model. Positive SES-MPD values indicate phylogenetic overdispersion of species, whereas negative values imply phylogenetic underdispersion or clustering. To explore visually the relationship between both phylogenetic estimates (ED, MPD) and elevation, we fitted linear and polynomial models in a similar way to that previously mentioned.

Lastly, we used the fuzzy set theory to scale up the phylogenetic relationships between species to the plot level and thereby, describe the phylogenetic composition of communities (Pillar and Duarte, 2010). Fuzzy set theory has been demonstrated to be a useful framework analysing metacommunity assembly patterns considering both functional and phylogenetic dimensions (Pillar et al., 2009; Duarte et al., 2016). In fuzzy sets, the elements have degrees of belonging to the set ranging in the interval from 0 to 1. The closer the degree of belonging is to 1, the more clearly the element

belongs to what is defining the set. Here, we employed phylogenetic fuzzy weighting (PFW), which defines fuzzy sets based on patristic distances (i.e., phylogenetic relatedness) among species, thereby generating a matrix describing the phylogeny-weighted species composition for each plot (matrix **P**). Thus, this matrix indicates the representativeness of different evolutionary lineages across the study sites (Duarte et al., 2016). The level of variation in phylogenetic diversity between plots was summarized into a dissimilarity matrix **D_p** (i.e., a resemblance matrix between pairs of communities computed from matrix **P**) that was regressed on the environmental variable using a modified version of the ADONIS method (McArdle and Anderson, 2001). Basically, this method allows to test (i) whether the environmental gradient affects the distribution of species across plots ('site shuffle'), and (ii) whether the association between the environmental gradient and the species distribution was phylogenetically structured ('taxa shuffle'). The 'taxa shuffle' null model allows for keeping species composition across plots constant while permuting only the phylogenetic relationships among taxa. This analysis was implemented in the R package *PCPS* (Debastiani and Duarte, 2014).

Relationship between phylogeny-free CWM and environment: null models

In a first step, we evaluated the phylogenetic signal in species traits by means of the Blomberg's *K* (Blomberg et al., 2003) and Pagel's λ statistics (Pagel, 1999), computed using the R package *phytools* (Revell, 2012). Both statistics were computed along with an associated *p*-value by comparing the observed data to a null distribution obtained by random perturbations (1,000 simulations) of the data. Values close to zero (i.e., *K* or $\lambda \sim 0$) indicate a lack of phylogenetic signal, while values close to unity indicate Brownian trait evolution.

Subsequently, we used Phylogenetic Generalized Least Squares (PGLS) to examine the influence of elevation and habitat on the mean values (CWM) of each trait (clutch size, number of breeding attempts, dispersal capacity and lifespan) across assemblages controlling for phylogenetic non-independence among species in relation to trait variation. However, CWM values computed for a set of communities do not constitute independent observations since some assemblages were more similar in species composition than others. Consequently, the association between raw CWM values and the environmental gradient may be prone to exhibit inflated type I error. That is, the analyses may be more influenced by species composition (species distribution across the plots) than by the trait variation itself (Duarte et al., 2018). To overcome this issue, Pillar and Duarte (2010) and Peres-Neto et al. (2017) suggested controlling for the influence of species composition on CWM variation using permutation-based null models tests. This method consists of two models (site-based and trait-based) that generate a null CWM distribution to be compared to the observed one (Duarte et al., 2018). The first model ('site shuffle') analyses whether the predictor (environmental) variable affects CWM. The second one ('trait shuffle' null model) freely permutes trait values across the species pool, while keeping species composition fixed in each assemblage in order to determine whether the environment-CWM relationship was mediated by trait distribution (environment $\rightarrow$ phylogeny $\rightarrow$ trait), which would indicate that both traits and species composition across communities are phylogenetically structured. That is, closely related lineages show similar traits in response to environmental variation also due to their shared evolutionary history. The other possibility is that the association between CWM and the environmental gradient is not affected by the phylogenetic composition of assemblages (matrix **P**), which would indicate lack of phylogenetic niche conservatism (environment $\rightarrow$ trait $\leftarrow$ phylogeny).

This approach was implemented using the ‘cwm.sig’ function developed by Duarte et al. (2018).

Results

Phylogenetic diversity, structure, and composition of communities

In terms of phylogenetic diversity, we found that community evolutionary distinctiveness (CED) scores showed a ‘hump-shape’ pattern with elevation, indicating that communities at mid-elevations (~1,500 m) tend to sustain species that represent a larger amount of unique evolutionary history (i.e., taxon with few close relatives) in comparison to those located at lower and higher elevations (Fig. 1a). There were no significant differences among habitat types (mean $\pm$ SE, alpine $n = 62$: 29.51 ± 1.99 ; farmland $n = 30$: 29.14 ± 1.97 ; forest $n = 59$: 29.62 ± 1.14) ($F_{2,148} = 0.95$, $p = 0.39$).

When testing for phylogenetic structure, we found a negative association between standardized Mean pairwise Phylogenetic Distance (*SES-MPD*) (values averaged over 8 yr) and elevation indicating that low elevation communities tend to exhibit lower phylogenetic clustering than those located at higher elevations ($\rho = -0.17$, $p = 0.03$). However, the relationship between *SES-MPD* and elevation was not linear, but sigmoidal; phylogenetic clustering increased up to 1,500 m, it subsequently decreased steeply coinciding with the treeline and then tended to increase again above 2,000 m (Fig. 1b). No community showed a significant positive *SES-MPD* value (indicating overdispersion), whereas 2-4 assemblages each year had values significantly negative ($p < 0.05$). Alpine assemblages exhibited a higher level of phylogenetic clustering (-0.22 ± 0.43) than forest and farmland assemblages (-0.05 ± 0.26 and -0.04 ± 0.33 , respectively) ($F_{2,148} = 4.52$, $p = 0.012$).

Phylogenetic fuzzy weighting showed that both elevation and habitat type affect the distribution of species across plots (*site shuffle*; $p < 0.05$ in 6 out of 8 years for both variables); nonetheless, such influence was not determined by the phylogenetic relationships among species in either case (*taxa shuffle*; $p > 0.05$ in all years) (Table 1).

Relationship between phylogeny-free CWM and environment: null models

All analyzed traits showed a significant phylogenetic signal regardless of the employed metric: Blomberg's K ($CS = 0.638$, $p = 0.001$; $NB = 0.388$, $p = 0.001$; $DIS = 0.780$, $p = 0.001$, $LS = 0.277$, $p = 0.005$) or Pagel's λ ($CS = 0.917$, $p < 0.001$; $NB = 0.809$, $p < 0.001$; $DIS = 0.990$, $p < 0.001$; $LS = 0.711$, $p = 0.001$).

Both community-weighted clutch size and lifespan tended to decrease with elevation due to both community composition (*site shuffle*) and through the similarity among species for these traits (*trait shuffle*) (Fig. 2a,b; Table 2). Both dispersal capacity and number of reproductive attempts per year showed a 'U-shaped' pattern when confronted with elevation; such influence was not determined by trait variation in either case (Fig. 2c,d; Table 2). Community-weighted lifespan varied among habitats partly due to differences in the phylogenetic composition of communities (Fig. 3; Table 2) whereas the effect of habitat on the remaining traits (clutch size, dispersal capacity and number of breeding attempts) was merely due to the distribution of species across study plots (Fig. 3; Table 2). Thus, the connection between life-history traits and the environment was independent of evolutionary history in most of cases.

Discussion

Understanding elevational gradients in phylogenetic diversity is vital for effective biodiversity conservation in the mountains, which are among the ecosystems most sensitive to the combined effects of climate and land-use change (Catalan et al., 2017). Although many authors have examined the phylogenetic structure of communities along altitudinal gradients in tropical mountains (Graham et al., 2009; Dehling et al., 2014; Boyce et al., 2019; Hanz et al., 2019), studies in the temperate region are much scarcer. Here, we observed that both elevation and habitat type affect the distribution of species across plots regardless of the phylogenetic relationships among species. This means that evolutionarily distant lineages responded similarly to environmental changes along the environmental gradient. Despite the lack of phylogenetic habitat filtering, we found trait convergence in response to environmental conditions; species inhabiting high elevation communities have smaller clutches and shorter lifespans than those conforming communities at lower elevations. Thus, alpine communities may have a lower potential to recover from perturbations, which is worrying under the current scenario of global warming.

Phylogenetic diversity, structure, and composition of communities

In terms of evolutionary distinctiveness (ED), we observed that passerine clades (e.g. finches Fringillidae, tits Paridae, stonechats Muscicapidae) contain species with lower ED scores (i.e., phylogenetically redundant species) than other parts of the tree (see Table S1 in Supplementary Material), which is consistent with higher diversification rates observed in songbirds (Jetz et al., 2012). In contrast, species-poor non-passerine groups tend to have higher values of ED. These “evolutionary distinctive” species do not share an overwhelming preference for a particular type of habitat; some of them are associated with forests (e.g. common cuckoo *Cuculus canorus*, wryneck *Jynx torquilla*,

hazel grouse *Bonasia bonasia*, golden oriole *Oriolus oriolus*) whereas some others inhabit open habitats (e.g. common swift, common quail *Coturnix coturnix*, Eurasian skylark *Alauda arvensis*). Consequently, we did not find differences in terms of community evolutionary distinctiveness among habitat types. The bird communities characterized by a large amount of evolutionary history were those located at mid elevation (1,500-1,700 m) probably due to it constituting a transition zone in which the ranges of species with different ecological requirements (low elevation species at their upper limit and high elevation species at their lower limit) overlap substantially. The mid-elevation peak in the number of species from phylogenetically distinct lineages does not support the idea that mountaintops represent refugia where we might expect to find relict lineages (Avise, 2004). Our findings are in concordance with that observed in a global scale study on the distribution of evolutionary distinctiveness in birds, which failed to find higher ED scores at high elevations (Jetz et al., 2014). Thus, although patterns described in other taxonomic groups (e.g. plants: Schönswetter et al., 2005; amphibians: Safi et al., 2013) are consistent with elevation facilitating the origination or immigration and persistence of ancient lineages, this idea may not hold in organisms with a higher dispersal capacity like birds.

Regarding phylogenetic structure, our results indicate that the level of phylogenetic dispersion tends to decrease as elevation and environmental harshness increase. However, only 3-4 communities per year (almost all located in alpine environments) showed values significantly negatives, which suggests a subtler effect of environmental filtering in comparison to that observed in tropical regions, where communities settled at high elevation showed significantly negative values (e.g. Graham et al., 2009; Dehling et al., 2014; Boyce et al., 2019; Hanz et al., 2019). This agrees with a recent global analysis of elevational gradients in phylogenetic diversity

(Montaño-Centellas et al., 2020). They observed more negative slopes -a stronger decline in mean phylogenetic distance with increasing elevation- in tropical mountains highlighting the existence of a latitude effect in the patterns of phylogenetic dispersion (Montaño-Centellas et al., 2020). This is probably due to the higher level of specialization of tropical bird species -frugivorous and/or nectarivorous species like hummingbirds- in comparison with those inhabiting more seasonal and less productive ecosystems at northern latitudes and which are more generalist and less dependent on plant communities (Dalsgaard et al., 2011; Jankowski et al., 2013; Vollstädt et al., 2017). Hence, the existence of a less steep decline of phylogenetic dispersion in temperate ecosystems suggests that the effect of environmental filtering in these regions may be less restrictive, allowing the establishment and persistence of a variety of lineages. An alternative but non-exclusive explanation may be the lack of competitively superior clades excluding other lineages in our study area. This latter possibility would reinforce the findings of a previous work, in which we conclude that interspecific competition does not seem to be a major force driving the structure of bird assemblages in the Swiss Alps (García-Navas et al., *submitted*).

From the results of phylogenetic fuzzy weighting it can be inferred that phylogeny does not have an important role as a structuring agent across plots. This finding disagrees with that previously observed in studies carried out with avian and butterfly communities in Brazil (Gianuca et al., 2014; Spaniol et al., 2019), which revealed the existence of ‘phylogenetic habitat filtering’ (i.e., lineages intrinsically linked to certain habitat types). According to our results, no clear phylogenetic composition was detected along habitat nor elevational gradients, which indicates that bird assemblages at low- and high elevation are composed of the same major lineages and that these are distributed in different habitat types. Thus, elevation itself is not

determinant for the distribution of certain clades; for example, we can find high-altitude adapted species in very different lineages including sparrows, pipits, thrushes, corvids and galliforms. This lack of phylogenetic structuring contrasts with that previously reported in terms of functional diversity in the same geographic region (García-Navas et al., 2020). Such a study revealed significant differences in functional diversity among habitat categories and provided evidence that the treeline represents an ecological barrier for the establishment and maintenance of some functional groups (García-Navas et al., 2020). Consequently, the different functional clusters do not group together into distinct phylogenetic lineages, which makes sense since the functional distance between a given species and its closest relative often did not correspond to the minimal observed phylogenetic distance (García-Navas et al., *unpubl. data*). The existence of discrepancies regarding patterns of functional and phylogenetic dispersions reinforces the view that phylogenetic information is complementary to the functional formation and both must be considered, as they represent two facets of biodiversity that are not redundant, but quite different (Cadotte et al., 2013; Luo et al., 2019).

Relationship between phylogeny-free CWM and environment: null models

All analyzed traits showed a significant phylogenetic signal, which indicates that these traits are relatively conserved across the phylogeny. Our results suggest that both elevation and habitat type shape life histories into suites of traits that are convergent among taxa facing the same environmental challenges (Laiolo and Obeso, 2017). Specifically, we found that CWM of clutch size (CS) and lifespan (LS) showed a clear decrease with increasing elevation, indicating that bird communities at high elevation are less productive and shorter-lived than those located at a lower elevation. This finding is counter to the trade-off or ‘resource economics’ theory according to which

one would expect that species with lower reproductive effort exhibit longer lifespan (i.e., allocation of resources to one purpose vs. another) (Stearns, 1976). Although the existence of reduced annual fecundity as elevation increases has been documented in several studies, probably as a consequence of temporal constraints imposed by a shorter breeding window and higher seasonality of resources in alpine environments (Balasubramaniam and Rotenberry, 2012; Lundblad and Conway, 2019), the relationship between LS and elevation is more controversial (see Boyle et al., 2016). Some studies testing for differences in adult survival among populations or species living at different elevation found a negative association between this trait and elevation (Lundblad and Conway, 2019), whereas some others did not find conclusive results (Badyaev and Ghalambor, 2001). The elevational patterns that two key traits like CS and LS exhibit, can explain the high turnover and the more dynamic nature of alpine bird communities (García-Navas et al., 2021). Thus, high elevation communities may be less resilient to environmental change; that is, they may have reduced capacity to recover from perturbations.

Community-weighted dispersal capacity (DIS) showed a ‘U-shaped pattern’ with a turning point around 1,700 m when plotted against elevation, indicating that communities at both extremes of the altitudinal gradient -those conformed by species associated to farmlands at low elevation and high-mountain specialists above 2,200 m- have higher dispersal capacity than communities located near the treeline ecotone (1,800-2,200 m; Gehrig-Fasel et al., 2007). It is noteworthy as species settled near this transition area are expected to move to higher elevations in order to track optimal abiotic conditions in response to warmer temperatures and/or woodland cover expansion (Ferrarini et al., 2017; Scridel et al., 2018). Consequently, it seems that

species that will be forced to change their ranges are those with the least potential to move, which is worrying from a conservation perspective.

Both elevation and habitat type affected the CWM of traits in most years. The association between elevation and traits was mediated by the phylogenetic history of species in the case of CS and LS, indicating that these traits were phylogenetically structured. On the contrary, the phylogenetic composition of assemblages only affected the habitat-lifespan relationship. Thus, the relationship between the remaining traits (CS, BS and DIS), and habitat type was not mediated by phylogenetic history, which suggest that the environment (habitat matrix) and phylogeny could both be correlated with species traits, but independently from each other. Such a circumstance may arise if the genetic component of these traits is subject to strong stabilizing selection. Overall, our results indicate that phylogenetic niche conservatism does not constraint bird community responses or adaptations to environmental change, at least with regard to three of the four studied traits. Despite the analyzed traits showing a significant phylogenetic signal, we observed that species with similar ecological preferences exhibited substantial patterns of trait convergence reinforcing the utility of considering phylogenetic and trait-based information jointly (Pavoine et al., 2014).

Lastly, it should be noted that we did not address the effect of intra-specific trait variation and exclusively followed a between-species comparison approach. Within-species variation may affect our results as some studies have shown that trait correlations under certain circumstances exhibit opposite signs within vs. across species due to ecotypic variation -genetic differentiation- or plasticity (see e.g. Pescador et al., 2015). However, the relative influence of intra-specific diversity tends to be much lower compared to that of the inter-specific component when there are substantial shifts in species composition (i.e., composition turnover) along the environmental gradient, as it

happens in our study system (Albert et al., 2011). At this point, we must also stress that our longevity data were derived from the literature, which is not elevation specific. Most species would have data biased to low elevation populations, and it is entirely feasible that high and low elevation populations of the same species could have different rates of survival. Lastly, a final caveat related to the scale and resolution of the environmental data; we categorized each 1km-square into one of the three habitat types (alpine, forest, or farmland), which could have masked a lot of variation and weakened the effect of phylogenetic niche conservatism, and used a single value (mean elevation) to characterize orographically each square, which entails a considerable loss of information. Consequently, our findings should be interpreted with some caution and ideally compared to those obtained at smaller scales in further studies to examine if they are consistent.

Conclusions

We found a higher degree of phylogenetic clustering in farmland communities and in those located at high elevation (above 2,000 m). However, the signal of phylogenetic clustering was weak (most values were >-1 and thus, statistically non-significant), which indicates that, in temperate systems, elevational gradients are probably less rigorous when it comes to lineage selection in comparison to those from tropical regions. Our findings suggest that co-occurring species are not particularly phylogenetically related, even though they share a similar response to abiotic conditions in terms of fecundity and longevity. Thus, although the existence of phylogenetic signal indicates that bird species belonging to the same clade tend to resemble each other more than less related taxa, for some traits there was stronger evidence for convergence among taxa that are more distantly related but co-occur in similar environments. The

lack of phylogenetic clustering contrast with that observed in terms of functional structure in a previous study (García-Navas et al., 2020) and suggests that a phylogenetic signal in traits *per se* does not necessarily imply a lack of trait convergence nor determine whether communities are likely to be phylogenetically structured (Pavoine et al., 2014). We can conclude that evolutionary constraints may not represent the most important driver of community assembly in our study system, a tendency also observed in other taxonomic groups with lower dispersal capacity (e.g. Spaniol et al., 2019). From a theoretical point of view, the present study provides support for the idea that the combination of phylogenetic and trait-based data allows a mechanistic insight into the processes that underpin the composition of communities along environmental gradients. From an applied standpoint, our work shows that high elevation communities, particularly those located around the treeline, are made up of short-lived species with low fecundity and low dispersal capacity which increases their ephemerality and makes them especially vulnerable to the effects of global change.

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Authors' contributions:

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

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The authors declare that they have no conflict of interest.

Ethics approval and consent to participate:

Not relevant

Consent for publication:

Not relevant

Availability of data and material:

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

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Figures

Figure 1. Relationship between a) Community Weighted Means for evolutionary distinctiveness and b) standardized effect size (*SES*) of Mean pairwise Phylogenetic Distance (MPD), and elevation in Alpine bird communities. *SES*-MPD is a metric of the randomness of community structure: negative values indicate community clustering, and positive values indicate community overdispersion. Each dot represents the mean value for each study plot ($n = 151$) averaged across eight years. Lines were fitted using third (x^3) and fifth order (x^5) polynomial models (grey areas indicate the 95% confidence interval), respectively. Those plots whose *SES*-MPD values were significant ($p < 0.05$) in more than 3 years are indicated with an orange circle.

Figure 2. Relationship between Community Weighted Means of a) clutch size, b) lifespan (estimated as maximum longevity), c) number of breeding attempts, and d) dispersal capacity (relation between body size and wing length) and elevation in bird communities of the Swiss Alps. Mean values for each plot averaged across eight years (1999, 2003, 2005, 2008, 2011, 2013, 2015 and 2018) are shown. Curves and grey areas depict the significant coefficient estimates ($p < 0.05$) and the 95% confidence intervals retrieved from linear (b, c), quadratic (d) or cubic (a) models.

Figure 3. Violin plots showing the kernel probability density of the data at different values to illustrate differences in Community Weighted Means of the four analyzed traits (clutch size, lifespan, number of breeding attempts and dispersal capacity) among habitats: alpine ($n = 62$), farmland ($n = 30$), and forest ($n = 59$). In all cases the proportion of habitat in which each plot was classified was higher than 50% (e.g, only those habitats with % of agriculture land > 50 were classified as farmlands). Violin plots

854 include a marker for the median of the data and a box for the interquartile range. A
855 topographic map with the location of the sampling plots across the study area and a
856 photograph of the different habitat categories are provided on the right. Photo credits: T.
857 Sattler.
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Table 1. Results of models testing for the influence of (a) elevation and (b) habitat on the distribution of species across plots without ('site shuffle', p_{site}) and after ('taxa shuffle', p_{taxa}) controlling for the phylogenetic relatedness among species. Under 'site shuffle', if the null hypothesis is rejected ($* = p_{\text{site}} < 0.05$), it can be concluded that elevation/habitat affects the distribution of species across study plots. Under 'taxa shuffle', if the null hypothesis is rejected, it can be concluded that the distribution of species across plots depends on the phylogenetic relatedness among them.

	year	Adj. R^2	F	p_{site}	p_{taxa}
(a) Elevation (dissimilarity matrix based on the mean elevation of each plot)					
	1999	0.26	48.87	0.001*	0.299
	2003	0.21	39.12	0.001*	0.303
	2005	0.27	55.27	0.001*	0.394
	2008	0.01	0.56	0.595	0.564
	2011	0.24	47.84	0.001*	0.444
	2013	0.23	45.72	0.001*	0.498
	2015	0.01	1.05	0.341	0.319
	2018	0.27	56.19	0.001*	0.404
(b) Habitat (dissimilarity matrix based on the proportion of farmland, forest and alpine habitat in each plot)					
	1999	0.28	18.03	0.001*	0.625
	2003	0.35	26.67	0.001*	0.150
	2005	0.31	22.71	0.001*	0.502
	2008	0.02	1.05	0.359	0.386
	2011	0.33	24.40	0.001*	0.422
	2013	0.32	23.10	0.001*	0.504
	2015	0.03	1.38	0.234	0.214
	2018	0.44	38.51	0.001*	0.191

		1999	2003	2005	2008	2011	2013	2015	2018
(a) Elevation	<i>Clutch size</i>								
(continuous variable)	<i>F</i>	180.16	11.02	184.91	0.80	187.38	194.47	1.52	207.30
	<i>p</i> _{site}	0.001*	0.001*	0.001*	0.370	0.001*	0.001*	0.225	0.001*
	<i>p</i> _{trait}	0.008*	0.593	0.037*	0.319	0.034*	0.039*	0.219	0.035*
	<i>NB</i>								
	<i>F</i>	54.12	0.01	49.09	1.64	61.07	56.89	1.12	67.26
	<i>p</i> _{site}	0.001*	0.941	0.001*	0.204	0.001*	0.001*	0.288	0.001*
	<i>p</i> _{trait}	0.263	0.988	0.389	0.187	0.324	0.387	0.282	0.322
	<i>Lifespan</i>								
	<i>F</i>	120.70	0.09	190.06	1.08	201.42	252.40	2.76	192.49
	<i>p</i> _{site}	0.001*	0.730	0.001*	0.292	0.001*	0.001*	0.091	0.001*
	<i>p</i> _{trait}	0.044*	0.972	0.029*	0.266	0.019*	0.024*	0.103	0.038*
	<i>Dispersal</i>								
	<i>F</i>	0.006	60.631	6.919	0.010	3.609	7.391	0.790	12.862
	<i>p</i> _{site}	0.939	0.001*	0.010*	0.928	0.061	0.007*	0.376	0.001*
	<i>p</i> _{trait}	0.990	0.186	0.779	0.912	0.829	0.762	0.345	0.726
(b) Habitat	<i>Clutch size</i>								
(discrete variable)	<i>F</i>	26.94	14.47	31.64	2.15	28.13	25.12	2.67	33.68
	<i>p</i> _{site}	0.001*	0.001*	0.001*	0.102	0.001*	0.001*	0.059	0.001*
	<i>p</i> _{trait}	0.342	0.536	0.331	0.078	0.339	0.416	0.056	0.319
	<i>NB</i>								
	<i>F</i>	12.46	10.65	14.37	2.43	15.11	12.97	2.06	15.09
	<i>p</i> _{site}	0.001*	0.001*	0.001*	0.054	0.001*	0.001*	0.101	0.001*
	<i>p</i> _{trait}	0.565	0.528	0.610	0.067	0.578	0.615	0.118	0.582
	<i>Lifespan</i>								
	<i>F</i>	44.69	11.62	48.92	1.57	56.68	50.71	3.27	62.76
	<i>p</i> _{site}	0.001*	0.001*	0.001*	0.213	0.001*	0.001*	0.026*	0.001*
	<i>p</i> _{trait}	0.152	0.501	0.132	0.164	0.087	0.130	0.034*	0.007*
	<i>Dispersal</i>								
	<i>F</i>	6.17	26.05	7.91	1.21	7.790	7.88	0.96	10.04
	<i>p</i> _{site}	0.002*	0.002*	0.001*	0.305	0.001*	0.001*	0.459	0.001*
	<i>p</i> _{trait}	0.777	0.211	0.785	0.233	0.775	0.749	0.376	0.723

889 **Table 2.** Linear models relating community-weighted means for four traits of birds -
 890 clutch size, number of breeding attempts, lifespan and dispersal capacity- to (a)
 891 elevation and (b) habitat type. The first model ('site shuffle') examines whether the
 892 environmental (predictor) variables affect CWM. The second model ('trait shuffle')
 893 analyses whether the association CWM-environment is mediated by the phylogenetic
 894 composition of communities (i.e., the evolutionary history shared by the species), which
 895 is possible when both traits and species composition across plots are phylogenetically

896 structured. Those cases in which the null hypothesis was rejected are indicated with an
897 asterisk.