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Variations in niche breadth and niche position of alpine birds along elevation gradients in the European Alps

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Research paper
Mountains support high levels of biodiversity, but they are also particularly vulnerable to climate change. Whilst studies on mountain biodiversity at the species level are common, studies that consider whole assemblages are scarce. We assessed how an alpine bird assemblage varied in terms of ecological habitat niche by surveying bird communities and habitat at point counts placed along elevation gradients in the Western Italian Alps. Niche breadth as measured by habitat use increased along the gradient, suggesting that being more generalist is an advantage in terms of survival at higher elevation. Niche position also increased with elevation, which means that species occurring at higher elevations use habitats that are atypical with respect to the average species in the community. Both niche breadth and position were negatively associated with habitat diversity, but these relationships were mainly driven by the species occurring at the very highest elevations (>2500 m), suggesting that true alpine specialist show a different pattern from the other species of the assemblage. Our results therefore generally supported the idea that having a wider niche breadth is useful in harsh environments, such as mountains, enabling the exploitation of a wider range of resources. The broader niche of many high elevation species may therefore indicate some degree of resilience to environmental change, as long as key habitat types are maintained.

Keywords
Alpine specialists, Birds, Elevation gradient, Niche breadth, Niche position.

INTRODUCTION
Climate change and land use changes are regarded as the major threats to biodiversity in the world (Travis, 2003; Stephens et al., 2016). The interaction between these two threats can intensify the impacts on biodiversity. Species are thus constrained to adjust their spatial distribution according to their ecological niches in order to have the resources they need to survive (Bani et al., 2019). It therefore follows that species with a broader niche (‘generalists’) will be better placed to adapt to
environmental changes (McKinney & Lockwood, 1999). Indeed, there are many examples of generalists increasing their range in response to environmental changes, often accompanied by decreases in narrow-niche specialists (e.g. Warren et al., 2001; Clavel et al., 2011). Studying niche breadth and niche position is thus likely to give an insight into those species that may be more vulnerable to environmental change in the future.

Birds are definitely a well-studied group regarding the impacts of environmental changes. Nevertheless, compared to other habitats, bird distribution and population dynamics are less well known in mountains (Chamberlain et al., 2012), mainly because of logistical constraints of working in this type of environment (Chamberlain et al., 2012). Mountains are subject to several pressures such as climate change (Gobiet et al., 2014), land-use change (Laiolo et al., 2004) and human disturbance (Caprio et al., 2011; Brambilla et al., 2016). Mountain species are considered particularly vulnerable to climate change, since opportunities to shift their distributions towards the mountain tops in response to environmental changes are constrained by mountain orography (i.e. they effectively run out of space on the ‘escalator to extinction’; (Freeman et al., 2018), and dispersal to alternative suitable sites may be limited by low connectivity with other mountain ranges (Lehikoinen et al., 2018).

Many species have already shown shifts in their distributions in response to environmental changes, notably towards high latitudes and elevations (Maggini et al., 2011; Reif & Flousek, 2012; Bani et al., 2019). These effects could have considerable consequences for mountain biodiversity (Chamberlain et al., 2013, 2016), and it has been shown that birds of high elevation are already declining in Europe (Lehikoinen et al., 2018). Given that habitat preference is one of the key ecological traits of any bird species (Reif et al., 2010), analysing how niche breadth and niche position can affect the distribution of species along environmental gradients is useful to understand and predict their future responses to environmental change. It may help to identify which species (i.e. with narrower niches, or that use less typical resources) may be negatively impacted by, and which species will be resilient to, future environmental change, if our environmental gradient is considered as a space-for
time substitution (Hodkinson, 2005; Blois et al., 2013). In the absence of long-term monitoring data, this approach can be useful to understand changes in the community.

Niche breadth and niche position are two complementary measures of specialisation. Niche position assesses how typical the resource use of a particular species is relative to all other species and the resources available. Thus, species with a high niche position use less typical resources, i.e. these species are specialised compared to the community studied (Mac Nally, 1989). Niche breadth measures the range of environmental conditions or habitat used by a species (Shugart & Patten, 1972).

As species that have a wide niche breadth show more tolerance to environmental conditions (Evans et al., 2011), they should be better adapted to higher elevations than species with a narrow niche breadth as conditions become harsher and less predictable (Körner, 2003). Furthermore, if species of high elevation are considered more generalist because of the environmental conditions, they should have a low niche position compared to other species. Furthermore, if niche trends only reflect habitat along the elevation gradient (i.e. habitat availability corresponds to habitat use), we also expect some relationship between habitat diversity and niche breadth.

Traditionally, the monitoring of biodiversity, including birds, has focused on the distribution or the abundance of single species. However, studying a whole community through assemblages such as habitat selection can be useful to assess ecosystem health (Siriwardena et al., 2019). We are unaware of any studies that have considered potential drivers of bird species distributions (including habitat and climate) along elevation gradients from a community perspective in the Alps. Here, we take an assemblage approach to consider how habitat niche varies along elevation gradients in the Western European Alps at relatively high elevation (1700-3100 m) using multi-species and multi-variate analyses. We define habitat niche (henceforth ‘niche’) as the environmental conditions present within a 100m radius (i.e. the point count area) in which a given species was detected, which include measures of habitat, topography and climate. We assume therefore that a given species is using the habitat resources as expressed by our niche measures at any point where it was recorded. This study focuses
on assessing the relationship (1) between niche (position and breadth) and elevation; (2) between niche (position and breadth) and habitat diversity.

METHODS

Study sites

A database of the presence of bird species from several sites in the Western Alps was compiled from two different bird surveys, carried out between 2010 and 2012 for the first, and in 2017 for the second. In the majority of cases, points were only surveyed in a single year (92%). Sites were located in the far north of Italy close to the French border (Appendix 1, Fig. S1). At a lower elevation, the European larch *Larix decidua* is the dominant species in the study area. The natural treeline is around 2200-2300 m, although in many areas, this limit is lower owing to pastoral activities. Juniper *Juniperus communis* and rhododendron *Rhododendron ferrugineum* are the main shrub species in the area. Above the treeline, alpine meadows and grasslands are found. Higher in elevation (>2700 m), rocks and scree are dominant (Chamberlain et al., 2016; Jähnig et al., 2018).

Point counts

Full methods are given in Chamberlain et al. (2013), so only a summary is provided here. Point counts were carried out from mid-May to mid-July along elevation gradients on transects that were a minimum distance of 300 m apart. On a single transect, each point was separated from another by at least 200 m to make sure two successive points did not overlap. All the points were above 1700 m (minimum = 1717 m) and reached a maximum of 3056 m. The mean range in elevation for each transect was 601 m ± 339 m (mean ± SD; n=39). At each point, for 10 minutes, all birds heard or seen were recorded by the observer within a 100 m radius (estimated with the aid of a laser range finder), and signs of potential breeding (e.g. singing, carrying nesting material or food for young, territorial disputes) were noted. Transects were visited one to three times. The maximum count over all visits
was used in the analyses for each species for the relatively small proportion of points that had more
than one visit.

Both studies (i.e. from 2010-2012 and 2017) adopted the same point count method, except that
the early survey included a 5-minute settling period before the point count period started, which was
absent in the later surveys. However, previous work (Chamberlain & Rolando 2014) and additional
analyses (Appendix 2) has demonstrated that inclusion of the settling period makes very little
difference to estimations of species occurrence. Observer effects were minimised since all observers
were experienced in identifying Alpine birds by sight and song, and the two surveys (i.e. from 2010-
2012 and 2017) were not independent and done in a consistent manner (one observer took part in
both and led training days for all observers to standardize the recording methods).

Two data sets were created, one with all the species observed and another one with only the
species showing evidence of potential breeding. In total, 39 transects were studied for 309 point
counts. During the first bird survey (2010-2012), 271 points were carried out in 34 transects. In 2017,
a total of 194 points were carried out on 35 transects in a restricted area (Natural Park of Val Troncea).
In order to avoid hyper-sampling from a single geographical location, only five transects comprising 38
points were selected, at random, from this latter data set. On average, there were 8 ± 4 (mean ± SD)
points per transect over the whole sample.

In order to carry out the multivariate analyses (CCA), points where no species were observed
(n=17 and n=35 respectively for complete and breeding data) and where habitat descriptions were
missing (n=15) were removed from both datasets, since this type of analysis cannot include zeros or
missing values. For the breeding data, 38 transects and 259 points were used, while for the complete
data, 38 transects and 277 points were used.

Environmental data

At each point count location, habitat was described within a 100 m radius (all variables are summarised
in Appendix 1). The percentage cover of each type of habitat was estimated by eye, including canopy
(vegetation above head height), shrubs (ligneous vegetation under head height), grassland (without canopy), rock (unvegetated areas and screes), and snow (surface that was still covered by snow during the survey). Such estimates have proven to match closely with those from remote-sensed land cover datasets (Chamberlain et al., 2013). The presence or absence of water, footpaths and dung was recorded. The number of mature trees (approximately greater than 20 cm in diameter at breast height) was recorded within a 50-m radius (in forested areas, it was not possible to count trees at a greater distance). The elevation of each point (in meters) was recorded with a GPS in the field. Topographic data (slope and aspect) were extracted from a Digital Terrain Model of Northern Italy. Slope was measured in degrees. Both northing and easting were considered and were expressed as an index equal to $-\cos(x)$ where $x$ is the aspect (north or east) in radians. A value of 1 indicates facing directly south (or east) and a value of -1 indicates facing directly north (or west).

Climate data were obtained from Chelsa (Climatologies at High resolution for the Earth’s Land Surface Areas) Climate (Karger et al., 2017). Data comprised monthly precipitation and temperature climatology for the period 1979-2013 and had a resolution of 30 arc sec. The mean monthly precipitation for the breeding season (May-July) was used. For temperatures, three variables were extracted: the minimum, maximum and mean monthly temperature for the breeding season.

**Data analysis**

All analyses were carried out in R 4.0.0 (R Core Team 2020). Preliminary analyses showed that including rare species (that occurred in less than 1% of the points) often resulted in convergence problems, hence these species were removed from the dataset in subsequent analyses (n=9 for complete data, n=5 for breeding data).

Following Reif et al. (2010) and Evans et al. (2011), habitat niche position and niche breadth were calculated using Canonical Correspondence Analysis (CCA) with environmental data (habitat and climate). CCA was performed using the `cca` command in the `vegan` package (Oksanen et al., 2013). CCA is a weighted ordination method, thus rare species have a low weight and do not have a great influence
in the rotation ordination. Elevation was not included as we were interested in explaining which environmental variables were the key drivers of assemblage change that may explain elevational trends. Using both habitat and climate variables to define the habitat niche of each species was justified by the fact that usually, models combining habitat and climate performed best to study species distribution along elevational gradients (Acharya et al., 2011; Chamberlain et al., 2016). The CCA allowed the niche breadth and the niche position of each species along the first four axes of the CCA (those explaining the largest proportion of variability in bird community structure) to be defined. Niche position was considered as “the distance of the centroid of a species from that of the whole assemblage (=mean of the coordinates of the species’ centroids)”. Niche breadth was calculated as the standard deviation of each species’ distribution of tolerance across each axis identified by the CCA, providing estimates of niche breadth. The root mean-squared standard deviations across the first four axes provided an overall estimate of niche breadth. To reduce the skew in their distribution and hence approximate normal distributions, niche position and niche breadth were log-transformed prior to analyses.

Habitat diversity was estimated at each point count with the percentage cover of each type of habitat, calculating the Shannon diversity index with the function diversity from the vegan package. Habitat diversity was estimated in elevation bands of 100 m (e.g. 1800-1899m) by calculating the mean Shannon index of all point counts located in each band.

Niche breadth and habitat niche position were modelled separately in relation to elevation, considering both linear and quadratic effects. The niche breadth and position of each species (extracted from the CCA – see above) were related to the median elevation (centred and scaled) across all points at which each species was recorded. In the same way, the relationship between niche breadth of each species and the standard deviation of elevation (centred and scaled) was analysed in order to see if species with a greater elevational range also have a wider niche breadth. Then, niche breadth and niche position were analysed in relation to habitat diversity along the elevation gradient.

In order to account for the non-independence of species due to a shared ancestry, we used a
Phylogenetic Generalised Least Squared (PGLS) approach for the analysis of niche breath and niche position. Closely related species are expected to have more similar traits because of their shared evolutionary history, and hence to produce more similar residuals from least squares regression. PGLS provides estimates of this covariance and includes it in a statistical model (Symonds & Blomberg, 2014). The PGLS approach was carried out in R using the *caper* package (Orme, 2018) and the phylogeny of Jetz et al. (2012).

Outliers were defined visually with a qq-plot (Mundry, 2014) and if outliers were detected, models were run again without these points. Both linear and quadratic models were fitted, and their performance was assessed using Akaike’s Information Criterion (AIC). The model with the lowest AIC was presented in the Results, unless the difference in AIC (ΔAIC) was less than 2, in which case they were considered as equivalent (Burnham & Anderson, 2010).

**RESULTS**

In total, 47 species were recorded, but only 34 of them showed signs of breeding (Table 1). There were 38 species recorded on at least 1% of the points (i.e. at least 3 records), of which 29 species showed evidence of potential breeding. Models were run for both datasets (complete and breeding records), but since the results were similar, only results for the complete dataset are presented here (see Appendix 3 for the main results with the breeding dataset).

**Species-habitat associations**

The first four axes of the CCA accounted for 76.5% of the variation in the data and represented the following gradients: (1) an elevation gradient from closed habitats (forest and shrubland) with light precipitation and relatively warm temperatures to open habitats (grasslands and rocks) with low temperatures and heavy precipitation (explaining 44.9% of the variation in the data); (2) from grassy and south exposed slope to rocky areas (14.9%); (3) from shrubby habitats to all other habitats (10.7%);
(4) from steep slopes with heavy precipitation to less steep areas with dung proving the presence of cattle (6.1%; see Appendix 4 for figures and Appendix 5 for the habitat scores on each axis).

*Niche position and niche breadth along the elevation gradient*

Niche position varied non-linearly with elevation (Fig. 1A; Appendix 6, Table S5), while niche breadth showed no association with elevation. However, after removal of one detected outlier (Snowfinch *Montifringilla nivalis*), there was a positive association between niche breadth and elevation (Fig. 1B; Table S5). Niche breadth was positively associated with the standard deviation of elevation in both linear and quadratic models (Fig. 2A) which performed equally ($\Delta$AICc<2; Table S5). Although Snowfinch was again identified as an influential outlier in the linear regression, its removal did not affect the outcome of the model (Table S5). Niche position varied non-linearly with the standard deviation of elevation (Fig. 2B, Table S5).

*Habitat niche position and niche breadth along the habitat diversity gradient*

Habitat niche position was negatively and linearly related to habitat diversity as measured by the Shannon index (Table S5). However, this relationship seemed to be mainly driven by three species (Alpine Accentor *Prunella collaris*, Snowfinch and Alpine Chough *Pyrrhocorax graculus*; Appendix 7, Fig. S3A). When these species were removed, habitat niche position was still negatively linked with habitat diversity, but the relationship was less strong (Table S5). Habitat niche breadth did not show any association with habitat diversity. However, an outlier was detected (Snowfinch), and removing this species resulted in a negative relationship between niche breadth and habitat diversity (Table S5). As previously, this trend was driven by few species (Alpine Accentor and Alpine Chough; Fig. S3B). When they were removed, there was no longer an evidence of a relationship between niche breadth and habitat diversity.

**DISCUSSION**
Habitat niche position and niche breadth along the elevation gradient

Habitat niche position increased with increasing elevation, suggesting that species occurring at higher elevations are associated with atypical habitats compared to the rest of the community, characterised by high precipitation, low temperatures, rock and grass. This result represents the turnover of species along the elevation gradient from forest species such as Chaffinch *Fringilla coelebs* and Tree Pipit *Anthus trivialis* to open habitat species such as Northern Wheatear *Oenanthe oenanthe* and finally high elevation species including Alpine Chough, Snowfinch and Alpine Accentor. García-Navas et al. (2020) showed that the alpine bird community (>2000 m) constituted a group distinct from lower elevation species (from 500 m to 2000 m) in terms of functional richness. However, they defined the treeline as the division between these two groups, whereas we found a continuum from forest species to open grassland species (from 1700 m to 2500 m), and then a more marked division for high elevation species (>2500 m).

Habitat niche breadth increased with increasing elevation, which supported our hypothesis that it is an advantage to be more generalist in a harsh environment, i.e. to be able to exploit a wider range of resources. Blondel & Farré (1988) found that specialisation of birds was more important in the early stages of ecological succession in open and semi-open forest than in mature forest. At first glance, the elevational gradient is similar to this ecological succession, with high elevation open habitat analogous to early stages and forests analogous to later stages at lower elevation. Thus, habitat niche breadth should have decreased with elevation. However, specialisation is only possible when environmental conditions are stable, and with increasing elevation the variability of some (particularly climatic) conditions increases. The elevation niche breadth hypothesis based on ecological succession as analogous to the habitat-elevation gradient is thus not supported. As for insects (Rasmann et al., 2014), a wider niche breadth is an advantage for birds at higher elevations. Furthermore, a narrower niche breadth at lower elevation could be explained by interspecific competition. Indeed, more species are living at low elevation and thus compete for the available resources. Due to competition between species, they have to reduce their niche (Fuller, 2012b).
For higher elevation species, the results indicate both a wide niche breadth and a use of less
typical habitats (i.e. a high niche position). These two results may at first sight seem contradictory, but
they arise because high elevation species use a range of habitats, but these habitats are not used by
the other species. Thus our high elevation species use a broad range of habitats, but these habitats are
atypical compared to the average species in the community.

Niche breadth and niche position increased with increasing standard deviation of elevation,
indicating as expected that species occupying a wider elevation range use a greater range of habitats
that are more typical of the community as a whole. Quintero & Jetz (2018) showed that there is globally
a mid-elevation peak in bird richness along elevation gradients which is mainly driven by wide-ranging
species. We did not observe this peak since our elevation gradient was not complete and already
started at relatively high elevation (c. 1700 m). When a species has a greater elevational range, it is
more likely that it will occupy a wider range of habitats since the elevational gradient is characterised
by a succession of habitats from forests to rocky and snowy areas.

Habitat niche position and niche breadth along the habitat diversity gradient
Habitat niche position was negatively associated with habitat diversity, but this trend was mainly
driven by three species of high elevation (Alpine Accentor, Alpine Chough and Snowfinch). At lower
elevations, more species are present because of a greater availability of resources while at higher
elevations, the number of species is very scarce. These species of high elevation differ a lot from the
whole assemblage of species in terms of habitat use and they usually occupy habitats with a low
diversity. Habitat niche breadth only showed an association with habitat diversity when species of high
elevation were included in the model. If habitat availability had matched perfectly with habitat use,
then we would have seen a positive relationship between habitat niche breadth and habitat diversity.
Instead the results imply that other factors also drive species distribution along this habitat diversity
gradient. Where habitat diversity is greater, more resources are available and it is likely that more
species can use them, but interspecific competition likely also increases with habitat diversity resulting
in species exploiting a narrower range of resources (i.e. having a narrower niche breadth; (Fuller, 2012b). Species of high elevation are less numerous (lower species richness) and thus the competition between them is lower, allowing them to exploit a wider range of resources (although Snowfinch was the exception to this pattern). Finally, there was little evidence for a gradient from low diversity habitat with ‘generalist’ species (broad niche breadth) to high diversity habitat ‘specialist’ species (narrow niche breadth); rather, there was an indication of a threshold that separated species of high elevation from the others. These species correspond to alpine specialists as defined by Thompson et al. (2012).

Alpine specialists are confined to the alpine zone (i.e. the major part of the population breeds in this zone), while alpine generalists breed in mountains, but they can also breed at lower elevation in different habitats. This result suggests that mountain generalists and mountain specialists may not show the same pattern regarding the link between habitat niche and habitat diversity.

Wider implications

The species with smaller habitat niches at lower elevations tended to be forest species. Although this may reflect a greater specialisation, these species are thought to be less threatened by climate change as upslope shifts in treelines are unlikely to result in a net loss of suitable habitats (or indeed suitable climates) in these species (Chamberlain et al., 2013). Species with a wider habitat niche breadth may adapt better to environmental change than species with a narrower habitat niche breadth (e.g. Evans et al., 2011), since they can exploit a larger range of resources. Indeed, there is evidence that generalist bird species are adapting to climate change better than specialist species (Davey et al., 2012; Pearce-Higgins et al., 2015; Bowler et al., 2019). Given that we found that habitat niche breadth increased with elevation, species at higher elevation should be fairly resilient to environmental change. This therefore suggests that high elevation species will have some capacity to adapt to environmental changes, including some currently relatively widespread grassland species likely to be negative affected by future climate change, e.g. Water Pipit *Anthus spinoletta*, Wheatear (Chamberlain et al., 2013), and Ring Ouzel *Turdus torquatus* (Beale et al., 2006). However, the greatest impact of climate
change for such species is likely to be the loss of suitable habitat caused by forest encroachment (García-Navas et al. 2020), hence such species may have some resilience, but only within habitat of suitable structure. Furthermore, according to our results, these habitats are atypical and hence only associated with higher elevation that are under threat from upslope shifts in vegetation zones. Strategies to minimise gross changes in habitat (e.g. maintaining open grasslands) may therefore be beneficial to these species, despite increases in temperature. In addition, some species occurring at the highest elevations did not seem to follow the general pattern. For example, among the three species occurring above 2500 m, Snowfinch, a scarce species, had a notably low habitat niche breadth, suggesting that this true high alpine specialist may indeed be particularly threatened (as per Scridel et al., 2018). Nevertheless, the two other species, Alpine Accentor and Alpine Chough, had particularly wide habitat niche breadths suggesting that they could adapt more easily to future environmental changes. Alpine Chough is indeed known to be adaptable and able to exploit anthropogenic habitats even at high elevation (Vallino et al., 2019).

Our results could be slightly biased by some factors. First, we were not able to account for detectability of species. Thus, we cannot know whether a species is rare because it has a low probability of detection or because it is indeed very scarce. That is particularly true for Snowfinch which was rarely contacted during the surveys and seemed to be specialised on high elevation habitats. Second, and similarly, some species known to be present in the area were detected only rarely, or not at all. For example, species such as Tengmalm’s Owl Aegolius funereus, Black Grouse Lyrurus tetrix or Rock Ptarmigan Lagopus muta have a lower detectability and are probably not suited to the point count method used. It would be interesting to get more data for these species in order to assess their influence on our analyses. Third, median elevation at which species occurred could be more accurately assessed if the abundance of each species had been estimated. Indeed, bird distributions do not show symmetric patterns along elevation gradients (Chamberlain et al., 2016), thus weighting presence of a species by the abundance would give a more precise median elevation for the species.
Finally, given that in theory, a species can vary remarkably in its occupancy rate of identical patches in different landscape contexts (Fuller, 2012a), more studies are needed in other regions of the Alps in order to corroborate our results and assess the transferability of our models. As Chamberlain et al. (2016) showed, species distribution is mainly driven by habitat and climate (and thus elevation), but much variation was still unexplained by their models, suggesting that other factors affected bird occurrence. Studying which factors (diet for example) can modulate bird occurrence along the elevation gradient could be the subject of further ecological studies on alpine birds. Furthermore, since niche space is multidimensional, it would also be useful to study the relationship between niche and elevation by using a broader niche definition including other factors such as diet or foraging substrate.

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CRAN: https://CRAN.R-project.org.


Fig. 1 Niche position (A) and niche breadth (B) in relation to the median elevation of each species’ range. The dashed lines are fitted from the models given in Table S2. For niche breadth, the influential outlier is represented by a bold black star with code in bold (Snowfinch). See Table 1 for species codes.
Fig. 2 Standard deviation of elevation in relation to habitat niche breadth (A) and niche position (B).

Influential outlier is represented by a bold black star with code in bold (Snowfinch). The orange line represents the prediction of the linear model (with all the species; Table S2). The green line represents the prediction of the quadratic model (with all the species; Table S2). See Table 1 for species codes.
Table 1 Number of records for each species contacted during the surveys (Count, given as all records/breeding records). Species with less than 3 records were removed from the data sets for analyses.

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