The role of climate in constraining the elevational range of the Water Pipit *Anthus spinoletta* in an alpine environment

Leandro Meléndez* & Paola Laiolo

Research Unit of Biodiversity (UO, CSIC, PA)

Oviedo University, Campus de Mieres

33600 Mieres, Spain

*Correspondence: leandro.melen@gmail.com

SUMMARY

The study of the determinants of species ranges along elevational gradients may shed light on the main ecological factors that constrain the species distribution and fundamental niche. In this study, we analyzed the abiotic and habitat predictors of the distribution of an alpine passerine, the Water Pipit (*Anthus spinoletta*), in its range in the Cantabrian Mountains, north-western Spain. We studied the influence of the climate, the habitat at different spatial scales and topography on the species' local density in mountain landscapes across a wide elevational gradient. We found that variables associated with spring and annual temperature values were the main determinants of Water Pipit density especially at the lower limit of the species' distribution (700-1200 m a.s.l.), where the species avoided areas that were altogether warmer. At high elevation sites (1600-2300 m a.s.l.), the main constraint to species' distribution was habitat structure and composition, with steep rocky areas being avoided by this alpine bird. The greatest densities were found in open but locally heterogeneous habitat at intermediate-high elevations, and the habitat variables that played a major role at the landscape scale were medium-tall shrublands and woodlands, but with contrasting effects depending on the elevation and the shape of the landscape areas considered. These results suggest that different sets of variables may constrain species density, and effects may differ at the upper and lower elevational limits, with the climate and the environment at the landscape scale being more important at lower elevations and the local habitat more important at higher elevations. In these settings, ongoing global warming is likely to cause an upward shift in the alpine species' range boundaries, but local habitat features could constrain the upward expansion, resulting in range contractions accompanying range shift.

Keywords

Climate change; distribution; density; elevational gradient; habitat selection; range shift.

INTRODUCTION

While the distributional patterns of organisms along latitudinal gradients have largely attracted the interest of ecologists, less studied are the altitudinal patterns of species distribution (Chamberlain et al. 2012, but see Rahbek 1997, Pounds et al. 1999, Nogués-Bravo et al. 2008, Popy et al. 2010). Certain abiotic and biotic patterns observed across latitudes may also occur across elevations (Stevens 1992), such as the northward and upward decrease in temperature, habitat and species diversity, and biotic interaction intensity (reviewed in Lomolino 2001). Climate has been identified as the main natural constraint to species expansion through range boundaries in both latitudinal and elevational gradients (Hughes 2000, Gaston 2003, McCarty 2001, Walther 2002, Araújo & Pearson 2005, Orme et al. 2006, Normand et al. 2009). In mountain systems, however, climatic conditions vary more sharply over distances than across latitudes, and ranges are more prone to be modulated by fine scale topographical features (orientation, slope, relief, etc.), which shape species distribution at a very local scale (Beniston 2003). On mountain tops, cold and extreme weather events might constrain the ranges of species via direct physiological constraints or limiting resources (Körner & Larcher 1988, Parmesan 2000, Beniston 2003, Martin & Wiebe 2004, Wingfield 2011), while milder climate at the lower fringes, with higher summer temperatures and lack of water, could have adverse physiological effects on cold-adapted species (e.g. Jump et al. 2006, Merrill et al. 2008, Wingfield 2011). At lower elevations, the human fingerprint is also more marked, and has produced large habitat and landscape changes, with important consequences on species ranges (Lomolino 2001).

Since mountains are among the terrestrial systems that have faced the greatest shifts in climatic conditions because of human activities (Schröter et al. 2005, Jump et al. 2006, Brunetti et al. 2009), the study of the distribution and density of alpine species along the elevational gradient and their dependence upon climate is of striking importance to predicting the vulnerability of mountain biodiversity (Körner 1999, Shoo et al. 2006). In this study we focus on the habitat and abiotic (climate and topography) determinants of the density of an alpine

species, the Water Pipit (*Anthus spinoletta*), along a broad elevational gradient (2000 m) embracing both Atlantic and Mediterranean climatic biozones in north-western Spain. As environmental determinants of the Water Pipit density we considered a set of climate and habitat variables at different spatial scales, including a local scale that approximates the species' territory and nearby areas (Bollmann et al. 1997) and a wider landscape scale embracing the territories of a local population. Our main prediction is that local climate significantly constrains the lower limit of alpine species distributions, and that local habitat features exert a stronger effect than landscape variables on the abundance of species with limited home ranges (Bollmann et al. 1997, Illera & Díaz 2006, García-del-Rey & Cresswell 2007, Maggini et al. 2011).

METHODS

Study area and species

The study was carried out in the Cantabrian Mountains, northern Spain. This mountain chain is about 300 km long and 50 km wide, it has a west-east orientation and includes several peaks above 2500 m a.s.l. These mountains represent the south-western limit of the alpine ecosystem in the Eurosiberian bioclimatic zone, and separate Atlantic from Mediterranean biota (Rivas-Martínez 1983). Our study area was located in the highest portions of the Cantabrian Mountains, in four massifs of the Picos de Europa National Park (Corisco, and Western, Central and Eastern Massifs; 43°07'- 43°16'N, 5°01'- 4°39'W, highest peak at 2648 m a.s.l.), which cover 16.925 ha. This area is characterized by a steep elevational gradient, with a vertical rise of 2400 m in very short linear distances (Fig. 1). The local climate is wet because of the influence of the Atlantic climate, particularly on the north-western slopes. Precipitation values range from 1000 to 1800 mm per year, and mean temperature from 4°C to 11°C per month. Clearance of forested areas has been intensive in historical times and lowered the treeline to 1000-1600 m a.s.l. Grazing by domestic livestock is widespread, pastoral abandonment is less

marked than in other mountains in Europe, and large extensions of pseudo-alpine open habitat occurs below the tree line (Jiménez et al. 2011, Blanco-Fontao et al. 2011).

The Water Pipit (*Anthus spinoletta*) is a short-distance insectivorous migrant and obligate ground-nesting alpine passerine. In Europe the species is highly dependent on alpine grasslands, occurring in open habitats above the treeline, preferring moist or wet meadows with pools, watercourses and snowfields (Tucker 1994, Bollmann et al. 1997, Cramp and Perrins 2004). In the Cantabrian Mountains the species' distribution and habitat are not well known, but its breeding has been reported at very low elevations (<1000 m a.s.l.) as compared to other European massifs (COA 2006-2007).

Field survey

We surveyed open habitats, which included pastures, alpine grasslands, shrublands and rocky areas. Since the species' distribution has not been described before, we surveyed the elevational range of 450 m (where large extensions of open pastures appear) to 2400 m a.s.l (where only rocky habitats cover the landscape). We established bird density using plot surveys (area count, Bibby et al. 2000), a method that is particularly useful for surveying birds in open terrains and abrupt landscapes (Laiolo et al. 2004; Caprio et al. 2011). We recorded all visual or aural detections (excluding fledglings) in 195 plots of 100 m radius (i.e. 3.14 ha) around the observer. Each plot was surveyed in a 10-minute period; for the first 5 minutes we performed a normal point-count (staying still), while the second five minutes of the survey was spent walking within the sampling plot to flush possible hidden individuals in shrubs or among the rocks. Plots were located in open areas with good visibility of the surroundings (over the 100 m radius of the plot). Each field day we walked a route in which we stopped five times (every 400 m, to avoid counting the same birds at multiple plots and to ensure independence of territories) to survey birds in plots of 100 m radius. The location of plots along daily depended on the ability to continue walking in the steep and rocky terrains of the area. Although we recognize that a random plot selection would be in theory ideal, in abrupt mountain areas this is not logistically feasible and plots are most often located following small trekking paths (see Laiolo et al. 2004; Fraterrigo & Wiens 2005; Caprio et al. 2011).

Plots were homogeneously distributed along the study elevational range (according to the area available to each elevational band of 200 m, and the percent of open habitat occurring in each band). Plot surveys were performed from 5 May to 20 July in 2009 and 2010, commencing just after sunrise and continuing for the following 5–6 hr. Plots were visited twice during the breeding season (early-middle breeding season, before the nestling phase), starting at lower altitudes to take into account the differences in bird breeding phenology. The lag between the two visits was on average $23 \pm 1.7(\text{SE})$ days (always within the same year). Water Pipit density was estimated as the maximum number of adults detected in each plot in the two surveys.

Determinants of Water Pipit density

Local habitat. Immediately after bird surveys, we estimated *in situ* the proportion of the main habitat types within plots (3.14 ha), to characterise the closest habitat to the territory (Bollmann et al. 1997). We visually established the percentage cover of grassland, shrub, trees and rock, and then obtained an index of habitat diversity (Shannon diversity index estimated from the percent cover of the different habitat types) (Table 1).

Local topographical variables. Elevation and UTM position of plots were measured with a GPS (Garmin eTrex Summit HC) in the field, while slope inclination, orientation, and shadiness (amount of direct sun exposure) were extracted from a digital elevation model grid (resolution 30 m) developed from satellite data (ASTER Global Digital Elevation Model V001) (Japan's Ministry of Economy, Trade and Industry and N.A.S.A.).

Local climate. Climatic determinants were estimated from layers of the Climate Atlas of the Iberia Peninsula (resolution 200 m; Ninzerola 2005) for each plot. The Climate Atlas was obtained from a model of 15 years of meteorological data from the local Meteorological National Institute stations and topographical variables such as slope inclination, orientation and elevation. We considered the minimum, mean and maximum temperatures and accumulated precipitation of April, May, June, July and August (corresponding to the reproductive period of the study species), the annual accumulated precipitation and annual mean, maximum and minimum temperatures. We also included the coefficients of variation of monthly parameters by dividing the standard deviation of climatic parameters in the five months by their average value.

Vegetation types at the landscape scale. We first considered as the “landscape scale” an area of 70 ha including the 5 plots surveyed in the same day along the same route, since they potentially hosted individuals from the same water pipit local populations (3 km was the maximum adult dispersal observed in the study area; $n = 866$ ringed individuals between 2009 and 2012, authors unpublished data). We selected 70 cells in a 100 x 100 m grid, using GIS software (ArcGIS 9.1) to create 39 landscape areas including five plots each (39×5 plots = 195 plots; Fig. 1). Since the shape of the area characterised by the above landscape areas changes according to the spatial distribution of plots, we characterized habitat variables also within 500 m-radius areas (78.5 ha) around each plots, to avoid landscape scale characteristics having a variable relationship with plots owing to their relative position along the route.

As habitat descriptors at the landscape scale we took into account the cover of the different vegetation types as estimated from the digital vegetation layers of the local Regional Governments (Asturias, Cantabria and Castilla-León) and the National Geographic Institute extracted from 1:25.000 National map series. Vegetation types were grouped into 10 categories that could be ecologically relevant for the species on the basis of previous knowledge of its habitat selection patterns (Table 1) (Tucker 1994, Bollman et al. 1997, Cramp & Perrins 2004): mature forest, secondary forest, heathlands, medium-tall legume shrublands, high-tall legume shrublands, dwarf-shrubs, pastures, alpine pastures, abandoned pastures and rocky areas. We estimated landscape diversity as the Shannon index of the proportion of the different habitat/vegetation types at this scale.

Data analysis

In contrast to habitat and topographical variables, which showed a weaker relationship between each other (habitat variables: $r < 0.54$; landscape variables: $r < 0.36$) and were entered in models as raw values, climate variables were highly and significantly correlated (temperature variables: $0.88 < r < 0.99$, all $P < 0.01$; precipitation variables: $0.27 < r < 0.94$, all $P < 0.01$; see Appendix S1 in Supporting Information). This redundancy was reduced by performing a Principal Component Analysis (PCA) to obtain independent climatic factors for models. Two single components were extracted, which explained over 92.7 % of the variance of the data set. The first component

(PC1) was highly and positively related with temperature variables (all correlations > 0.99) and showed a weaker correlation with precipitation variables (all correlations < 0.51); it was therefore defined as the “temperature factor” in keeping with loading significance (Perez-Neto et al. 2003) (Appendix S2). The second component (PC2) showed weak correlations with temperature variables (< 0.18) and stronger correlations with precipitations (> 0.70); hereafter we define it as the “precipitation factor” (Appendix S2).

We tested habitat (local and landscape), topographic and climatic determinants on Water Pipit density by means of generalized additive mixed models (GAMMs; Wood 2012), which allow the incorporation of random effects when observations are grouped in clusters, in our case the route (site), and the year of study. GAMMs are flexible and effective in nonlinear regression analysis and permit modelling the shape of the response curve as a series of smoothing splines dictated by the data (Suárez-Seoane et al. 2002), and testing each main effect after controlling for the other determinants. We first used a Combining Conditional Expectations and Residuals (CERES) plot, in order to visualize curvilinear relationships with determinants (Cook 1998) (see Appendix S3); these determinants were then entered as smooth variables in GAMMs. As usual in counts, a Poisson distribution of errors was used.

Models were built with a stepwise selection method based on a "backward/forward" selection and the Akaike information criterion AIC, in order to find the most probable models (accounting for the lowest AIC). This selection method starts with the full model and eliminates predictors one at a time, at each step considering whether the AIC will be improved by adding back in a variable removed at a previous step. Models resulting from the stepwise selection procedure that were separated by less than 2 AIC points from the model with the lowest AIC were considered as having substantial support in the data, and were therefore equally discussed (Burnham & Anderson 2002). As recommended in Symonds & Moussalli (2011), to better interpret the relative likelihood of each model, given the data and each model set, we carried out a model averaging based on the AIC values and extracted the “Akaike weight” (w_i), expressing the weight of evidence in favour of each model (Burnham & Anderson 2002). Weights for all models combined add up to 1.

All the analyses were performed with the software R version 2.15 (R Core Team 2012); the package *glmm4* was used to carry out the GAMMs.

RESULTS

Variation in Water Pipit density along the elevational gradient

We recorded the occurrence of the Water Pipit in 107 plots, corresponding to 54.9% of the plots surveyed. The average density in occupied plots was 1.67 individuals/plot (0.53 individuals/ha). The highest elevation at which we found a Water Pipit territory was 2240 m a.s.l.; the lowest altitude was 750 m. The species was found only in 18.5% of the plots located below 1000 m. The number of plots occupied at the lower fringes of the species' distribution (low elevations: 750-1200 m a.s.l.) was 48.9%, 68.2% at intermediate altitudes (medium elevations: 1200-1600 m), and 66.6% at the upper boundaries (high elevations: 1600-2300 m). Differences were significant between low and medium elevations ($\chi^2_1=4.50$, $P=0.034$) and between low and high elevations ($\chi^2_1=4.32$, $P=0.037$), but not between medium and high elevations ($\chi^2_1=2.83$, $P=0.092$).

A non-linear relation between Water Pipit density and elevation resulted (GAMM: $s(\text{elevation}): \text{edf}=3.16$, $F=8.19$, $P<0.001$). Density peaked at medium elevations (1200-1600 m: 1.55 ± 0.22 SE individuals per plot) and declined in lower (750-1200 m: 0.74 ± 0.13 SE) and higher elevations (1600-2300 m: 0.93 ± 0.09 SE) (one-way ANOVA, $F_{2, 168}=17.37$, $P<0.001$) (Fig. 2).

Climate and habitat determinants at two spatial scales

The best models explaining the Water Pipit density mainly included local habitat and climate features (the “temperature factor” of PCA: PC1), either when considering landscape variables estimated in 70 ha areas around five survey plots (Table 2) or considering 500 m-radius areas around each survey plot (Appendix S4). The relationship between density and the “temperature factor” was negative in all models: the lowest densities occurred where PC1 was highest (e.g.

mild temperature) and the highest densities where PC1 lowered to intermediate-cold temperatures (Fig. 3).

Density was also affected by pasture cover (in the two best probable models of the set of three) and habitat diversity (all best models), both variables being significantly and positively associated with Water Pipit density (Table 2; Appendix S4). Conversely, tree cover (all models), slope inclination, shrub and rock cover (two models each) were negatively associated with density (Table 2; Appendix S4). None of the habitat variables at the landscape scale was included in any best model of species density (Table 2; Appendix S4).

To better disentangle the role of temperature and habitat in determining Water Pipit abundance at the species elevational boundaries, we tested for the importance of climatic and habitat factors at the three elevational bands where the species occurs (750-1200 m, low elevations; 1200-1800 m, intermediate elevations; 1800-2200 m, high elevations) by performing three sets of GAMMs. At low elevations the temperature factor negatively affected species density, while grassland cover and habitat diversity had a positive effect when considering the landscape scale around 5 study plots (Table 3). In models entering landscape variables in 500 m-radius areas the temperature factor had no more effect (Appendix S5), and some habitat predictors at this scale affected Water Pipit density (negative effect of woodland cover and positive effect of medium-tall legume shrubland cover Appendix S5). At intermediate elevations, the precipitation factor positively affected Water Pipit density, while tree cover had a negative effect (Table 3). Landscape variables had a mayor effect when considering the 500 m-radius areas, with a positive effect of woodland cover and medium-tall legume shrublands cover (Appendix S5). At high elevations, density was only associated with habitat characteristics and the effect of temperature and precipitation was no longer significant; here, rock cover was negatively correlated with species density, while habitat diversity positively affected it at both landscape levels here considered (Table 3; Appendix S5).

DISCUSSION

The local variation of Water Pipit density was not linear along the elevational gradient. We found an initial increase of species density when passing from the lower to the intermediate limits of the species distribution, and a stabilization or moderate decline from medium elevations to mountaintops. Thus, at the lowest elevations the species becomes less abundant, but the same trend was not observed at the highest extreme of the distribution, where the species still occur in good numbers (Fig. 2). As observed in a variety of montane and alpine vertebrates, different factors appear to constrain the lowest and highest elevational limits of the species distribution (Galbreath et al. 2009, Jankowski et al. 2010, Gifford & Kozak 2012). In the case of the Water Pipit, density was mostly constrained by temperature and landscape variables (depending of the shape of the landscape area) at low elevations, and by local habitat features at high elevations.

The importance of climate variables

Temperature was the most important predictor of species density, and the negative effect of this climatic variable peaked at the lowest elevations when considering the landscape scale embracing 5 survey plots. The decrease in density at warm temperatures could depend on several climate-driven mechanisms. First, there may be direct effects of the temperature on individual physiology, with increasing physiological stress in warm climates (Barbosa et al. 2007, Gifford & Kozak 2012). These effects might be associated with increased energy costs of vital functions, which eventually may reduce individual performance in populations at lower elevations (Wingfield 2011). Alternatively, individual performance may drop as a result of the high pathogen abundance and diversity in warmer climates (Rohde and Heap 1998, Guègan et al. 2003 and 2005, Guernier et al. 2004, Garamszegi 2011), or more complex/richer communities of competitors and predators (Jankowski et al. 2010). At low elevations, predation (in the form of increased adult and nest predation rates), and competition with species with superior skills in exploiting resources (Schwartz 1992, Newton 1998, Davis et al. 1998) may negatively affect the fitness of Water Pipits. Indeed, in our study mountains, bird species' richness and overall density decline with elevation and increase with temperature, and this may carry important consequences for climate-driven species' interactions (Juárez 2010).

Alternatively, prey available for the Water Pipit may increase with elevation. For instance, the presence of snow patches in spring at high elevations offer the study species (as well as several other alpine passerines, such as *Montifringilla nivalis*, *Prunella collaris* and *Pyrrhocorax graculus*) a source of insects trapped in snow that may be important for feeding young (Antor 1995, Rolando & Laiolo 1997, Laiolo & Rolando 1999). The weak decline of Water Pipit density in the highlands was not apparently due the negative effect of the coldest temperatures (Fig. 3), but to habitat characteristics (Table 3), as detailed below.

The importance of the habitat

The best candidate models explaining Water Pipit density suggested that the environment hosting the highest abundance of the Water Pipit in the Cantabrian Mountains presented high pasture cover and some shrubs, rocks and trees in little proportions. Heterogeneous open habitats show the highest densities of the Water Pipit in other European regions as well (Rauter & Reyer 2002, Cramp 2004), and also favor several other open-habitat passerine species (Illera 2001, Laiolo 2005, Laiolo et al. 2011). Indeed, grassy habitats with some diversity of vegetation may support great abundance of prey for the Water Pipit, and nest sites may be better hidden (Brodmann et al. 1997). In contrast to the great influence of local habitat features, landscape composition played a minor role in determining the overall density of the Water Pipit in our study area, a phenomenon that confirms that habitat selection may occur at very small scales in passerines of small size (Serrano & Astrain 2005, Illera et al. 2010).

It has been reported that at the highest elevations, extreme weather events during breeding, such as late snowfalls and freezing, may cause high nest mortality in the Water Pipit and constrains its density (Rauter & Reyer 2000, Bollmann & Reyer 2001). However, in our study system, the proximity of the sea and the limited elevations may limit the occurrence of these events. Instead, the high cover of unsuitable rocky habitats is the factor that apparently plays a more important role in limiting Water Pipit density at higher elevations. The Cantabrian Mountains, especially in their eastern portion, have a steep topography and rocky nature; they are the favorite breeding habitats for crevice-nesting alpine birds (Jiménez et al. 2013), but may not favor those alpine species depending on alpine prairie availability both for nesting and

feeding, such as the Water Pipit (Rauter et al. 2002). The fact that Water Pipit density, but not occurrence, was limited in the highest elevations partially supports the idea that bottom-up effects (resource limitation) may be constraining species density at higher elevations (Körner & Larcher 1988, Parmesan 2000, Beniston 2003).

The importance of topography and the habitat at the landscape scale

Apart from the effect of elevation, which was discussed above, slope also affects Water Pipit density, being this species more abundant in the flattest plots, and avoiding the steepest areas at high elevations. Steep slopes in the alpine or nival belts accumulate scarce organic matter owing to soils being younger and unstable, a fact that conditions their overall productivity (Huber et al. 2007) and may, in turn, prevent the Water Pipit to settle. Precipitation can increase the productivity of these high elevation soils (Gottfried et al. 1998), thus also (partially) explaining the Water Pipit selection for the wettest plots in certain conditions (Table 3).

The effects of the habitat at the landscape scales are puzzling, depending on the shape of the landscape area considered, and varying according to the range of elevations considered. The former finding highlights the difficulties in identifying the proper scale and range of distances from the survey plots to define the environment at the landscape scale (Mitchell et al. 2001). It also suggests that the Water Pipit density in a plot may be more likely constrained by the closest habitats around territories rather than by the environment of the local populations, as possibly occurring in species using direct rather than indirect (social) cues of environmental quality when establishing territories (Laiolo & Tella 2006). Notably, the landscape scale was more important in the lowlands, where the highest diversity of environments is found (Jimenez et al. 2013)

CONCLUSIONS

This study suggests that the distribution and density patterns of the Water Pipit in its southern range boundaries is highly conditioned by climatic factors, mainly by the PCA factor related with temperatures at the lower limits of the species distribution and by the PCA factor related with precipitation at intermediate elevations. Habitat availability and composition at the local scale play a major role at the upper boundary of the species distribution, whereas the landscape exerts a less straightforward effect.

Since the Cantabrian Mountains (together with the Pyrenees) represent the southern limit of the alpine ecosystem in the Euro-Siberian region (Rivas-Martínez 1983), its alpine belt is expected to suffer the greatest changes in climatic conditions and biotic functions in the next few decades (Thuiller et al. 2005, Huntley et al. 2007). An increase in temperature could cause an upward range shift in many species (Wilson et al. 2007, Lenoir et al. 2008, Maggini et al. 2011, Pauli et al. 2012), but local habitat features could constrain upward expansions, resulting in range contractions accompanying range shifts, and the increase of small and fragmented island populations in mountains (Körner 1999, Freppaz et al. 2010). Although at a global scale the largest range shifts are expected to occur in the colder distribution margins at high latitudes (Thomas & Lennon 1999, Brommer 2004 but see Zuckerberg et al 2009, Parmesan et al. 1999, Chen et al 2009), the limited area of the alpine biozone in our study area (squeezed between the Mediterranean climate to the south and the oceanic climate to the north), together with the restricted elevations of its mountains, may not maintain viable populations of alpine species in changing climatic conditions.

ACKNOWLEDGMENT

We are grateful to Mónica García, Oscar Magaña, Gerardo Jiménez, Natalia Juárez and Marta Lomas for field assistance, and the Picos de Europa National Park for providing permissions to work in the protected area. We also thank Javier Seoane and Jordi Moya, who greatly assisted in statistical analyses, two anonymous referees and Simon Butler for providing useful comments on an early version of the manuscript. Sarah Young kindly checked the English. The research was funded by grants of Fundación Biodiversidad and MICINN (CGL2011-28177) to PL.

REFERENCES

- Antor, R.J.** 1995. The importance of arthropod fallout on snow patches for the foraging of high-alpine birds. *Journal of avian biology* **26**: 81-85.
- Araújo, M.B. & Pearson, R.G.** 2005. Equilibrium of specie's distributions with climate. *Ecography* **28**: 693–695.

- Barbosa, A., Merino, S., Benzal, J., Martínez, J. & García-Fraile, S.** 2007. Population variability in heat shock proteins among three Antarctic penguin species. *Polar Biology* **30**: 1239-1244.
- Beniston, M.** 2003. Climatic change in mountain regions: a review of possible impacts. *Climatic Change* **59** (1/2): 1573-1480.
- Bibby, C.J., Burgess, N.D., Hill, D.A. & Mustoe, S.H.** 2000. *Bird Census Techniques*. 2nd edition. Academic Press, London.
- Blanco-Fontao, B., Quevedo, M. & Obeso, J.R.** 2011. Abandonment of traditional uses in mountain areas: typological thinking versus hard data in the Cantabrian Mountains (NW Spain). *Biodiversity and Conservation* **20**: 1133-1140.
- Bollmann, K., Reyer, H. & Brodmann, P.** 1997. Territory quality and reproductive success: can Water Pipits (*Anthus spinoletta*) assess the relationship reliably. *Ardea* **85**: 83–98.
- Bollmann, K. & Reyer, H.U.** 2001. Reproductive success of Water Pipits in an Alpine environment. *Condor* **103**: 510-520
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.S.S.** 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* **24**: 127-135.
- Brodmann, P. A., Reyer, H. U. & Baer, B.** 1997. The Relative Importance of Habitat Structure and of Prey Characteristics for the Foraging Success of Water Pipits (*Anthus spinoletta*). *Ethology* **103**: 222-235.
- Brommer, J. E.** 2004. The range margins of northern birds shift polewards. *Ann. Zool. Fennici*. **41**: 391-397.
- Brunetti, M., Lentini, G., Maugeri, M., Nanni, T., Auer, I., Böhm, R. & Schöener, W.** 2009. Climate variability and change in the Greater Alpine Region over the last two centuries based on multi-variable analysis. *International Journal of Climatology* **29**: 2197-2225.
- Burnham, K.P. & Anderson, D.R.** 2002. *Model selection and multi model inference: a practical information-theoretic approach*. Springer-Verlag, New York.
- Caprio, E., Chamberlain, D.E., Isaia, M. & Rolando, A.** 2011. Landscape changes caused by high altitude ski-pistes affect bird species richness and distribution in the Alps. *Biological Conservation* **144**: 2958-2967.
- Chamberlain, D., Arlettaz, R., Caprio, E., Maggini, R., Pedrini, P., Rolando, A. & Zbinden, N.** 2012. The altitudinal frontier in avian climate impact research. *Ibis* **154**: 205-209.
- Chen I-C, Shiu H-J, Benedick S, Holloway JD, Chey VK, Barlow, H.S., Hill, J.K. & Thomas, C.D.** 2009. Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proc Natl Acad Sci USA*. **106**: 1479-1483.
- C.O.A.** 2006. *Annuariu Ornitolóxicu d'Asturies*, 1999. *El Draque* **6**: 140-141.

- C.O.A.** 2007. *Anuariu Ornitolóxicu d'Asturies*, 2000. *El Draque* 7: 178-179.
- Cook, R.D.** 1998. *Regression Graphics: Ideas for Studying Regeressions Through Graphics*. Wiley, New York.
- Cramp, S., & C. M. Perrins, editors.** 2004. *The birds of the western Palearctic*. Volumes VII and VIII. Oxford University Press, Oxford, UK.
- Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B. & Wood, S.** 1998. Making mistakes when predicting shifts in species range in response to global warming. *Nature* **391**: 783-786.
- Fraterrigo, J.M. & Wiens, J.A., 2005.** Bird communities of the Colorado Rocky Mountains along a gradient of exurban development. *Landsc. Urban Plann.* **71**: 263–275.
- Freppaz, M., Filippa, G., Caimi, A., Buffa, G. & Zanini, E.** 2010. Soil and plant characteristics in the alpine tundra (NW Italy). In Gutierrez, B. and Pena, C. (eds.) *Tundras: Vegetation, Wildlife and Climate Trends*, 81-110. New York: Nova Science Publishers.
- Galbreath, K.E., Hafner, D.J. & Zamudio, K.R.** 2009. When cold is better: climate-driven elevation shifts yield complex patterns of diversification and demography in an alpine specialist (American pika, *Ochotona princeps*). *Evolution* **63**: 2848-2863.
- Garamszegi, L.** 2011. Climate change increases the risk of malaria in birds. *Global Change Biology* **17**: 1751-1759.
- García-del-Rey, E. & Cresswell, W.** 2007. The breeding biology of the endemic Berthelot's Pipit *Anthus berthelotii* in a harsh oceanic island environment (Tenerife, Canary Islands). *Ostrich* **78**: 583-589.
- Gaston, K.J.** 2003. *The Structure and Dynamics of Geographical Ranges*. Oxford University Press, Oxford, UK.
- Gifford, M.E. & Kozak, K.H.** 2012. Islands in the sky or squeezed at the top? Ecological causes of elevational range limits in montane salamanders. *Ecography* **35**: 193–203.
- Guernier, V., Hochberg, M. E., & Guégan, J.-F.** 2004. Ecology drives the worldwide distribution of human diseases. *PLOS Biol.* **2**: 0740-0746.
- Huber, E., Wanek, W., Gottfried, M., Pauli, H., Schweiger, P., Arndt S.K., Reiter, K., & Richter, A.** 2007. Shift in soil-plant nitrogen dynamics of an alpine-nival ecotone. *Plant Soil* **301**:65-76
- Hughes, L.** 2000. Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution* **15**: 56-61.
- Huntley, B. Green, R.E., Collingham, Y.C. & Willis, S.G.** 2007. *A Climatic Atlas of European Breeding Birds*. Lynx Edicions, Barcelona.
- Ihaka, R. & Gentleman, R.** 1996. R: a language for data analysis and graphics. *Journal of Computational and Graphical Statistics* **5**: 299-314.

- Illera, J.C.** 2001. Habitat selection by the Canary Islands stonechat (*Saxicola dacotiae*) (Meade-Waldo, 1889) in Fuerteventura Island: a two-tier habitat approach with implications for its conservation. *Biological Conservation* **97**: 339-345.
- Illera, J.C., Díaz, M. & Nogales, M.** 2006. Ecological traits influence the current distribution and range of an island endemic bird. *Journal of Biogeography* **33**: 1192-1201.
- Illera, J.C., Von Wehrden, H. and Wehner, J.** 2010. Nest site selection and the effects of land use in a multi-scale approach on the distribution of a passerine in an island arid environment. *Journal of Arid Environment* **74**: 1408-1412.
- Jankowski, J.E., Robinson, S.K. & Levey, D.J.** 2010. Squeezed at the top: Interspecific aggression may constrain elevational ranges in tropical birds. *Ecology* **91**: 1877-1884.
- Jiménez, G., Meléndez, L., Blanco, G. & Laiolo, P.** 2013. Dampened behavioral responses mediate birds' association with humans. *Biological Conservation* **159**: 477-483.
- Juárez, N.** 2010. Gradientes altitudinales de diversidad de aves en el Parque Nacional de los Picos de Europa: determinantes ambientales y climáticos. Master Project, University Pablo Olavide, Sevilla.
- Jump, A.S., Hunt, J.M. & Peñuelas, J.** 2006. Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Global Change Biology* **12**: 2163-2174.
- Körner, C. & Larcher, W.** 1988. 'Plant Life in Cold Climates', in Long, S. F. and Woodward, F. I.(eds.), *Plants and Temperature*, The Company of Biol Ltd, Cambridge, 25-57.
- Körner, C.** 1995. Impact of atmospheric changes on alpine vegetation: the ecophysiological perspective. In Guisan, A., Holten, J.I., Spichiger, R. and Tessier, L., editors, *Potential ecological impacts of climate change in the Alps and Fennoscandian mountains*, Geneve: Ed. Conservatoire & du Jardin Botaniques de Genève 13-120.
- Körner, C.** 1999a. Why are there global gradients in species richness? Mountains might hold the answer. *Trends in Ecology and Evolution* **15**: 513-514.
- Körner, C.** 1999b. *Alpine Plant Life*, Springer-Verlag, Heidelberg and New York, 338 pp.
- Laiolo, P. & Rolando, A.** 1999. The diet of the Chough (*Pyrrhocorax pyrrhocorax*) and the Alpine Chough (*Pyrrhocorax graculus*): seasonality, resource partitioning and population density. *Rev. Ecol. (Terre Vie)*. **54**: 133-147.
- Laiolo, P., Dondero, F., Ciliento, E. & Rolando, A.** 2004. Consequences of pastoral abandonment for the structure and diversity of the alpine avifauna. *Journal of Applied Ecology* **41**: 294-304.
- Laiolo, P.** 2005. Spatial and seasonal patterns of bird communities in Italian agroecosystems. *Conservation Biology* **19**: 1547-1556.
- Laiolo, P., Obeso, J.R. & Roggia, Y.** 2011. Mimicry as a novel pathway linking biodiversity functions and individual behavioural performances. *Proceedings of the Royal Society B*. **278**: 1072-1081.

- Laiolo, P., & Tella J.L.** 2008. Social determinants of songbird vocal activity and implications for the persistence of small populations. *Animal Conservation* **11**: 433–441.
- Lenoir, J., Gegout, J. C., Marquet, P. A., De Ruffray, P. & Brisse, H.** 2008. A significant upward shift in plant species optimum elevation during the 20th century. *Science* **320**: 1768-1771.
- Lomolino, M.** 2001. Elevation gradients of species-density: historical and prospective views. *Global Ecology and Biogeography* **10**: 3-13.
- Maggini, R., Lehmann, A., Kéry, M., Schmid, H., Beniston, M., Jenni, M. & Zbinden, N.** 2011. Are Swiss birds tracking climate change?: Detecting elevational shifts using response curve shapes. *Ecological Modelling* **222**: 21-32.
- Martin, K. & Wiebe, K.L.** 2004. Coping mechanisms of alpine and arctic breeding birds: extreme weather and limitations to reproductive resilience. *Integrative and Comparative Biology* **44**: 177-185.
- McCarty, J. P.** 2001. Ecological Consequences of Recent Climate Change. *The Journal of the Society for Conservation Biology* **15**: 320-331.
- Merrill, R.M., Gutiérrez, D., Lewis, O.T., Gutiérrez, J., Díez, S.B. & Wilson, R.J.** 2008. Combined effects of climate and biotic interactions on the elevational range of a phytophagous insect. *Journal of Animal Ecology* **77**: 145-155.
- Midgley G, Hannah, L., Millar, D., Thuiller, W. & Booth, A.** 2003. Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region. *Biological Conservation* **112**: 87-97.
- Mitchell, M.S., Lancia, R.A., & Gerwin, J.A.,** 2001. Using landscape-level data to predict the distribution of birds on a managed forest: effects of scale. *Ecological Applications* **11**: 1692–1708.
- Newton, I,** 1998. *Population Limitation in Birds*. Academic Press, London.
- Ninyerola, M., Pons, X. & Roure, J.M.** 2005. *Atlas Climático Digital de la Península Ibérica. Metodología y aplicaciones en bioclimatología y geobotánica*. Ed. Universidad Autónoma de Barcelona, Bellaterra.
- Nogues-Bravo, D., Araujo, M.B., Romdal, T. & Rahbek, C.** 2008. Scale effects and human impact on the elevational species richness gradients. *Nature* **453**: 216-219.
- Normand, S., Treier, U.A., Randin, C., Vittoz, P., Guisan, A. & Svenning, J.C.** 2009. Importance of abiotic stress as a range-limit determinant for European plants: insights from species responses to climatic gradients. *Global Ecology and Biogeography* **18**: 437-449.
- Orme, C.D.L., Davies, R.G., Olson V.A., Thomas, T.H., Ding, T.S., Rasmussen** <http://www.plosbiology.org/article/info%3Adoi%2F10.1371%2Fjournal.pbio.0040208> - **aff6** **P., Ridgely, R.S., Stattersfield, A.J., Bennett, P.M., Owens, I.P., Blackburn, M.M. & Gaston, K.J.** 2006. Global Patterns of Geographic Range Size in Birds. *PLoS Biology* **4**: 208.

- Parmesan C, Ryrholm N, Steefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L, Kullberg J, et al.** 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* **399**: 579-83.
- Parmesan, C., Root, T. L. & Willig, M. R.** 2000. Impacts of extreme weather and climate on terrestrial biota. *Bulletin-American Meteorological society*. **3**: 443–450.**Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Alonso, J.L.B., Coldea, G., Dick, J., Erschbamer, B., Calzado, R.F., et al.** 2012. Recent Plant Diversity Changes on Europe's Mountain Summits. *Science* **336**: 353-355.
- Pearson, R. G. & Dawson, T. P.** 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* **12**: 361-371.
- Perez-Neto, P. Jackson, D.A. & Somers, K.M.** 2003. Giving meaningful interpretation to ordination axes: assessing loading significance in principal component analysis. *Ecology* **84**: 2347–2363
- Piersma, T., A. Lindstrom, R. H. Drent, I. Tulp, J. Jukema, R. I. G. Morrison, J. Reneerkens, H. Schekkerman, & G. H. Visser.** 2003. High daily energy expenditure of incubating shorebirds on high arctic tundra: A circumpolar study. *Functional Ecology* **17**: 356-362
- Popy, S., Bordignon, L. & Prodon, R.** 2010. A weak upward elevational shift in the distributions of breeding birds in the Italian Alps. *Journal of Biogeography* **37**: 57-67.
- Pounds, J.A., Fogden, M.P.L. & Campbell, J.H.** 1999. Biological response to climate change on a tropical mountain. *Nature* **398**: 611-615.
- R Core Team,** 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- Rahbek, C.** 1997. The relationship among area, elevation, and regional species richness in neotropical birds. *The American Naturalist* **149**: 875-902.
- Rauter, C. M., Reyher, H. & Bollmann, K.** 2002. Selection through predation, snowfall and microclimate on nest-site preferences in the Water Pipit, *Anthus spinoletta*. *Ibis* **144**: 433-444.
- Rauter, C. & Reyher, H.U.** 2000. Thermal and energetic consequences of nest location and breeding times in Water Pipits (*Anthus spinoletta*). *Journal fur Ornithologie* **141**: 391-407.
- Reynolds, R.T., Scott, J.M. & Nussbaum, R.** 1980. A variable circular-plot method for estimating birds numbers. *Condo*. **82**: 309-313.
- Rivas-Martínez, S.** 1983. Pisos Bioclimáticos de España. *Lazaroa* **5**: 33-43.

- Rohde, K., & M. Heap.** 1998. Latitudinal differences in species and community richness and in community structure of metazoan endo- and ectoparasites of marine teleost fish. *International Journal of Parasitology* **28**: 461-474.
- Rolando, A. & Laiolo, P.** 1997. A comparative analysis of the diets of the Chough *Pyrrhocorax pyrrhocorax* and the Alpine Chough *Pyrrhocorax graculus* co-existing in the Alps. *Ibis* **139**: 388-395.
- Schröter, D., Cramer, W., Leemans, R., Prentice, I.C., Araújo, M.B., Arnell, N.W., Bondeau, A., Bugmann, H., Carter, T., Gracia, J.G., et al.** 2005. Ecosystem service supply and vulnerability to global change in Europe. *Science* **310**: 1333-1337.
- Schwartz, M.W.** 1992. Modeling the effect of habitat loss on potential rates of range change for trees in response to global warming. *Biodiversity and Conservation* **2**: 51-61.
- Shoo, L.P., Williams, S.E. & Hero, J.M.** 2006. Detecting climate change induced range shifts: where and how should we be looking? *Austral Ecology* **31**: 22-29.
- Symonds, M.R.E. & Moussalli, A.** 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology* **65**: 13-21.
- Stevens, G.C.** 1992. The Elevational Gradient in Altitudinal Range: An Extension of Rapoport's Latitudinal Rule to Altitude. *The American Naturalist* **140**: 893-911.
- Suárez-Seoane, S., Osborne, P.E. & Alonso, J.C.** 2002. Large-scale habitat selection by agricultural steppe birds in Spain: identifying species-habitat responses using generalized additive models. *Journal of Applied Ecology* **39**: 755-771.
- Thomas, C.D. & Lennon, J.J.** 1999. Birds extend their ranges northwards. *Nature*. 399: 213.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., et al.** 2004. Extinction risk from climate change. *Nature* **427**: 145-148.
- Thomas, J.A., Rose, R.J., Clarke, R.T., Thomas, C.D. & Webb, N.R.** 1999. Intraspecific variation in habitat availability among ectothermic animals near their climatic limits and their centres of range. *Functional Ecology* **13**: 55-64.
- Thuiller, W., Lavorel, S., Araujo, M., Sykes & M. Prentice, C.** 2005. Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences* **102**: 8245-8250.
- Tucker, G.M. & Heath, M.F.** 1994. *Birds in Europe*. Their conservation status. Birdlife International, Cambridge, UK.
- Walther, G.R., Post, E., Convey, P., Menze, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O. & Bairlein, F.** 2002. Ecological responses to recent climate change. *Nature* **416**: 389-395.

- Wilson, R. J., Gutiérrez, D., Gutiérrez, J. & Monserrat, V. J.** 2007. An elevational shift in butterfly species richness and composition accompanying recent climate change. *Global Change Biology* **13**: 1873-1887.
- Wingfield, J., Kelly, P. & Angelier, F.** 2011. What are extreme environmental conditions and how do organisms cope with them?. *Current Zoology (in press)*.
- Wood, S.N.** 2012. gamm4: Generalized additive mixed models using mgcv and lme4. R package version 0.1-6. <http://CRAN.R-project.org/package=gamm4>.
- Zuckerberg, B., Woods, A., & Porter, W.F.** 2009. Poleward shifts in breeding bird distributions in New York State. *Global Change Biology* **15**: 1866-1883.

Table 1. List of the determinants of Water Pipit density entered in models.

Variable	Measurement	Species	Scale
Temperature factor	PCA factor (minimum, average and maximum temperature from April to August and annual average per plot)		Plot
Precipitation factor	PCA factor (accumulated precipitation from April to August and total annual precipitation per plot)		Plot
Pasture cover	Relative percentage of grasslands cover	All grasslands and herbaceous species (pastures, meadows, alpine grasslands formations, etc.)	Plot
Tree cover	Relative percentage of canopy trees	All tree species (e.g. <i>Fagus sylvatica</i> , <i>Quercus robur</i> , <i>Fraxinus excelsior</i> , <i>Salix</i> spp., <i>Crataegus monogyna</i> , <i>Ilex aquifolium</i> , <i>Sorbus</i> spp., <i>Corylus avellana</i> , etc.)	Plot
Shrub cover	Relative percentage of shrubland cover	All shrub species (<i>Genista legionensis</i> , <i>Ulex europaeus</i> , <i>Erica</i> spp., <i>Daboecia cantabrica</i> , <i>Juniperus communis</i> subsp. <i>alpina</i> , etc.)	Plot
Rock cover	Relative percentage of rock and scree cover		Plot
Habitat diversity	Shannon index of habitat diversity ($H' = -\sum p_i \times \ln p_i$, where p_i is the relative frequency of observations of the species i)		Plot
Slope	The average slope inclination in degrees per plot		Plot
Exposure	The main orientation per plot (north, south, east and west)		Plot
Shadiness	Number of hours without direct sun exposure per plot		Plot
Altitude	In meters above the sea level		Plot
Latitude	UTM. European datum 1950		Plot
Longitude	UTM. European datum 1950		Plot
Woodlands	Relative Percent area covered by woodland	<i>Fagus sylvatica</i> , <i>Quercus robur</i> , <i>Fraxinus excelsior</i> , <i>Alnus glutinosa</i> , <i>Castanea sativa</i> , <i>Prunus avium</i> , etc.	Landscape
Secondary forest	Relative percent area covered by young, open forested areas with regenerating trees	<i>Salix</i> spp., <i>Crataegus monogyna</i> , <i>Ilex aquifolium</i> , <i>Sorbus</i> spp., <i>Corylus avellana</i> , etc.	Landscape (70ha)
Heathlands	Relative percent area covered by heath formations	Shrublands dominated by <i>Erica</i> spp., <i>Daboecia cantabrica</i> and <i>Calluna vulgaris</i>	Landscape
Medium-tall legume shrublands	Relative percent area covered by medium-tall shrub formations	Mainly formations of <i>Ulex europaeus</i> , <i>Genista hispanica</i> , <i>Genista florida</i> , <i>Cytisus cantabricus</i> , etc.	Landscape
High-tall legume shrublands	Percentage area cover by medium-tall shrub formations	<i>Genista scoparius</i> , <i>Retama sphaerocarpa</i> .	Landscape
Dwarf-shrubs	Relative percent area covered by dwarf and creeping scrubs	Shrublands of <i>Juniperus communis</i> subsp. <i>alpina</i> , <i>Genista legionensis</i> , <i>Arctostaphylos uva-ursi</i> , etc.	Landscape
Pastures	Relative percent area covered by meadows and pastures	Very complex herbaceous formations (e.g. <i>Carex</i> spp., <i>Festuca</i> spp., <i>Cynosurus cristatus</i> , <i>Juncus articulatus</i> , <i>Luzula nutans</i>)	Landscape
Abandoned pastures	Percentage area cover by abandoned pastures	Formations of ferns (mainly <i>Pteridium aquilinum</i>) and brambles (<i>Rubus</i> spp. and <i>Rosa</i> spp.)	Landscape
Alpine meadows	Percentage area cover by alpine meadows	High altitude meadow formations (mixture of communities dominated by <i>Nardus stricta</i> and <i>Festuca burnatii</i>)	Landscape
Rocky areas	Percentage area cover by rocks and screes	Rock desert communities	Landscape
Landscape diversity	Shannon index of landscape category diversity ($H' = -\sum p_i \times \ln p_i$, where p_i is the relative frequency of observations of the species i)		Landscape

Table 2. Best candidate models explaining variation of Water Pipit density. Models were separated by < 2 AIC points from the model with the lowest AIC. The site and the year were entered as random factors. The Estimate, Standard Error (SE) and Z-test value were presented for each predictor. The estimated degrees of freedom (edf) and Chi-square value were presented for the smooth term. A Poisson distribution of errors and log link function was used. The AIC and the Akaike weights (ω_i) for each model are also shown. Landscape variables for this set of models were estimated in 70 ha areas surrounding five survey plots. For models with landscape variables estimated in 500 m-radius circular areas around each survey plots see Appendix S6.

Best candidate models

Predictors	Estimate	SE	Z
<i>Pasture cover at the plot scale</i>	0.015	0.003	4.04
<i>Canopy tree cover at the plot scale</i>	-0.075	0.024	-3.08
<i>Habitat diversity at the plot scale</i>	0.997	0.270	3.69
<i>Slope at the plot scale</i>	-0.017	0.009	-1.78
Smooth term:		edf	X²
<i>s(temperature factor)</i>		3.62	13.44
AIC = 174.06 n = 195; ω_i = 0.52			

Predictors	Estimate	SE	Z
<i>Pasture cover at the plot scale</i>	0.01	0.003	4.07
<i>Canopy tree cover at the plot scale</i>	-0.07	0.021	-2.99
<i>Habitat diversity at the plot scale</i>	1.01	0.271	3.71
Smooth term:		edf	X²
<i>s(temperature factor)</i>		3.68	14.55
AIC = 175.40; n = 195; ω_i = 0.27			

Predictors	Estimate	SE	Z
<i>Canopy tree cover at the plot scale</i>	-0.08	0.025	-3.46
<i>Habitat diversity at the plot scale</i>	0.91	0.250	3.54
<i>Shrub cover at the plot scale</i>	-0.01	0.004	-3.32
<i>Rocky cover at the plot scale</i>	-0.01	0.004	-3.42
Smooth term:		edf	X²
<i>s(temperature factor)</i>		3.79	18.01
AIC = 175.82; n = 195; ω_i = 0.21			

Table 3. List of the best candidate models explaining variation in Water Pipit density at three elevational bands. Models were separated by < 2 AIC points from the model with the lowest AIC. The site and the year were entered as random factors. The Estimate, Standard Error (SE) and Z-test value were presented for each predictor. The estimated degrees of freedom (edf) and Chi-square value were presented for the smooth term. A Poisson distribution of errors and log link function was used. The AIC and the Akaike weights (ω_i) for each model are also shown. Only data from plots above the minimum elevation of the species were entered in models. Landscape variables for this set of models were estimated in 70 ha areas surrounding five survey plots. For models with landscape variables estimated in 500 m-radius circular areas around each survey plots see Appendix S7.

Low elevations (750-1200 m)			
Predictors	Estimate	SE	Z
<i>Pasture cover at the plot scale</i>	0.02	0.008	2.16
<i>Habitat diversity at the plot scale</i>	1.52	0.650	2.32
<i>Temperature factor</i>	-1.27	0.620	-2.03
AIC = 52.45 n = 47; ω_i = 1			
Medium elevations (1200-1800 m)			
Predictors	Estimate	SE	Z
<i>Canopy tree cover at the plot scale</i>	-0.08	0.04	-1.99
<i>Precipitation factor</i>	0.41	0.210	1.97
AIC = 55.76; n = 44; ω_i = 0.64			
Predictors	Estimate	SE	Z
<i>Pasture cover at the plot scale</i>	0.08	0.030	2.77
<i>Shrub cover at the plot scale</i>	0.07	0.030	2.38
<i>Rocky cover at the plot scale</i>	0.09	0.030	2.76
<i>Precipitation factor</i>	0.44	0.170	2.57
AIC = 56.91; n = 44; ω_i = 0.36			
High elevations (1800-2200 m)			
Predictors	Estimate	SE	Z
<i>Rocky cover at the plot scale</i>	-0.01	0.004	-3.31
<i>Habitat diversity at the plot scale</i>	0.88	0.320	2.73
AIC = 64.45; n = 82; ω_i = 0.46			
Predictors	Estimate	SE	Z
<i>Pasture cover at the plot scale</i>	0.02	0.004	3.42
<i>Habitat diversity at the plot scale</i>	1.13	0.320	3.46
AIC = 64.15; n = 82; ω_i = 0.54			

Figure captions:

Fig.1. Map of the study area showing the distribution of the 39 70-ha survey sites (white polygons) in eastern Cantabrian Mountains.

Fig.2. Partial-residual plots for the generalized additive mixed model (GAMM) for Water Pipit density as a function of elevation. The y axis represents the residuals from regressing Water Pipit density against all the independent variables except X_i and X_i . $[i]$ = residuals from regressing X_i against the remaining independent variables. The effect on Water Pipit density is shown on the y-axis and is represented as a spline (s) of elevation. Estimated degrees of freedom are in the parentheses on the y-axis. The trend line and the 95 % confidence interval are also shown.

Fig.3. Partial-residual plots for the generalized additive mixed model (GAMM) for Water Pipit density as a function of the temperature factor (PC1). The effect on Water Pipit density is shown on the y-axis and is represented as a spline (s) of the temperature factor. Estimated degrees of freedom are in the parentheses on the y-axis. The trend line and the 95 % confidence interval are also shown.

1

2 Figure 1

3

4

7
8 Figure 3

9
10
11

Additional Supporting Information (ON-LINE)

Appendix S1. Correlations between the climatic variables considered in this study (r-values are shown).

Correlation matrix														
	Annual minimum temperature	April average temperature	May average temperature	June average temperature	July average temperature	August average temperature	Annual accumulated rainfall	April accumulated rainfall	May accumulated rainfall	June accumulated rainfall	July accumulated rainfall	August accumulated rainfall	Temperature coefficient of variation	Rainfall coefficient of variation
Annual minimum temperature	1	0.991	0.991	0.987	0.983	0.987	-0.152	0.383	-0.49	-0.485	0.001	0.355	-0.965	0.144
April average temperature	0.991	1	1	0.998	0.996	0.998	-0.097	0.418	-0.438	-0.455	0.031	0.386	-0.964	0.145
May average temperature	0.991	1	1	0.999	0.996	0.999	-0.106	0.412	-0.443	-0.456	0.029	0.381	-0.964	0.143
June average temperature	0.987	0.998	0.999	1	0.999	1	-0.099	0.393	-0.446	-0.462	0.005	0.353	-0.964	0.17
July average temperature	0.983	0.996	0.996	0.999	1	0.999	-0.091	0.384	-0.448	-0.468	-0.017	0.333	-0.963	0.198
August average temperature	0.987	0.998	0.999	1	0.999	1	-0.096	0.398	-0.443	-0.462	0.01	0.358	-0.966	0.166
Annual accumulated rainfall	-0.152	-0.097	-0.106	-0.099	-0.091	-0.096	1	0.634	0.826	0.624	0.587	0.55	0.147	-0.171
April accumulated rainfall	0.383	0.418	0.412	0.393	0.384	0.398	0.634	1	0.48	0.302	0.744	0.919	-0.323	-0.175
May accumulated rainfall	-0.49	-0.438	-0.443	-0.446	-0.448	-0.443	0.826	0.48	1	0.909	0.753	0.501	0.471	-0.496
June accumulated rainfall	-0.485	-0.455	-0.456	-0.462	-0.468	-0.462	0.624	0.302	0.909	1	0.724	0.389	0.488	-0.659
July accumulated rainfall	0.001	0.031	0.029	0.005	-0.017	0.01	0.587	0.744	0.753	0.724	1	0.857	0.039	-0.724
August accumulated rainfall	0.355	0.386	0.381	0.353	0.333	0.358	0.55	0.919	0.501	0.389	0.857	1	-0.296	-0.491
Temperature: coefficient of variation	-0.965	-0.964	-0.964	-0.964	-0.963	-0.966	0.147	-0.323	0.471	0.488	0.039	-0.296	1	-0.146
Rainfall: coefficient of variation	0.144	0.145	0.143	0.17	0.198	0.166	-0.171	-0.175	-0.496	-0.659	-0.724	-0.491	-0.146	1

Appendix S2. A) Eigenvalues and percentage of variance explained by a Principal Component Analysis performed to reduce climatic variables. B) Correlations between raw climatic variables and the first two PCA factors (PC1 and PC2).

A) Eigenvalues and Total Variance Explained

Component	Initial Eigenvalues			Extraction sums of Squared Loadings		
	Total	% of variance	% Cumulative	Total	% of variance	% Cumulative
PC1	19.206	73.87	73.87	19.206	73.870	73.870
PC2	4.893	18.818	92.688	4.893	18.818	92.688

B) Correlation between Factors and raw variables (Varimax Rotated Component Matrix)

	Component	
	PC1	PC2
Annual accumulated rainfall	-0.073	0.809
April accumulated rainfall	0.372	0.820
May accumulated rainfall	-0.416	0.868
June accumulated rainfall	-0.511	0.704
July accumulated rainfall	0.314	0.893
August accumulated rainfall	-0.005	0.972
April average temperature	0.998	-0.018
May average temperature	0.998	-0.024
June average temperature	0.998	-0.042
July average temperature	0.996	-0.061
August average temperature	0.998	-0.043
April maximum temperature	0.992	0.027
May maximum temperature	0.993	-0.026
June maximum temperature	0.983	-0.106
July maximum temperature	0.930	-0.186
August maximum temperature	0.956	-0.151
April minimum temperature	0.994	-0.009
May minimum temperature	0.994	-0.009
June minimum temperature	0.994	0.005
July minimum temperature	0.994	0.011
August minimum temperature	0.991	0.010
Annual minimum temperature	0.997	-0.030
Annual maximum temperature	0.997	-0.059
Temperature coefficient of variation	-0.916	0.093
Rainfall coefficient of variation	0.146	-0.756

Appendix S3. CERES plots of the variables included in the best GAMMs testing for variation in Water Pipit density. CERES plots represent the estimate of the partial residual plots, showing the curve of the relationship between the dependent variable to each predictor (green line).

Appendix S4. Best candidate models explaining variation of Water Pipit density entering landscape variables estimated in 500 m-radius circular areas around each plots. Models were separated by < 2 AIC points from the model with the lowest AIC. The site and the year were entered as random factors. The Estimate, Standard Error (SE) and Z-test value were presented for each predictor. The estimated degrees of freedom (edf) and Chi-square value were presented for the smooth term. A Poisson distribution of errors and log link function was used. The AIC and the Akaike weights (ω_i) for each model are also shown.

Best candidate models

Predictors	Estimate	SE	Z
<i>Pasture cover at the plot scale</i>	0.015	0.003	4.04
<i>Canopy trees cover at the plot scale</i>	-0.075	0.024	-3.08
<i>Habitat diversity at the plot scale</i>	0.997	0.270	3.69
<i>Slope inclination at the plot scale</i>	-0.017	0.009	-1.79
Smooth term:		edf	X²
<i>Temperature factor</i>		3.620	13.40
AIC =174.06; n = 195; ω_i = 0.44			

Predictors	Estimate	SE	Z
<i>Pasture cover at the plot scale</i>	0.015	0.003	4.20
<i>Canopy trees cover at the plot scale</i>	-0.070	0.025	-3.00
<i>Habitat diversity at the plot scale</i>	0.948	0.285	3.32
<i>Dwarf-shrubs cover at the landscape scale</i>	-0.592	0.657	-0.90
Smooth term:		edf	X²
<i>Temperature factor</i>		3.550	14.99
AIC =174.39; n = 195; ω_i = 0.37			

Predictors	Estimate	SE	Z
<i>Canopy trees cover at the plot scale</i>	-0.086	0.025	-3.46
<i>Shrub cover at the plot scale</i>	-0.015	0.004	-3.32
<i>Rocky cover at the plot scale</i>	-0.015	0.004	-3.42
<i>Habitat diversity at the plot scale</i>	0.913	0.258	3.54
Smooth term:		edf	X²
<i>Temperature factor</i>		3.790	18.01
AIC =175.82; n = 195; ω_i = 0.18			

Appendix S5. List of the best candidate models explaining variation in Water Pipit density at three elevational bands. The landscape variables were estimated in 500 m-radius circular areas around each plot. Models were separated by < 2 AIC points from the model with the lowest AIC. The site and the year were entered as random factors. The Estimate, Standard Error (SE) and Z-test value were presented for each predictor. The estimated degrees of freedom (edf) and Chi-square value were presented for the smooth term. A Poisson distribution of errors and log link function was used. The AIC and the Akaike weights (ω_i) for each model are also shown. Only data from plots above the minimum elevation of the species were entered in models.

Low elevations (750-1200 m)

Predictors	Estimate	SE	Z
<i>Pasture cover at the plot scale</i>	0.028	0.01	2.76
<i>Canopy cover at the plot scale</i>	-0.052	0.036	-1.47
<i>Habitat diversity at the plot scale</i>	1.793	0.732	2.45
<i>Woodland cover at the landscape scale</i>	-6.634	4.255	-1.56
<i>Medium-tall shrubland at the landscape scale</i>	6.476	3.192	2.03

AIC = 44.12; n = 47; ω_i = 0.39

Predictors	Estimate	SE	Z
<i>Pasture cover at the plot scale</i>	0.025	0.01	2.61
<i>Habitat diversity at the plot scale</i>	1.555	0.669	2.32
<i>Woodland cover at the landscape scale</i>	-10.334	4.449	-2.32
<i>Medium-tall shrubland at the landscape scale</i>	5.351	3.088	1.73

AIC = 44.50; n = 47; ω_i = 0.37

Predictors	Estimate	SE	Z
<i>Pasture cover at the plot scale</i>	0.0186	0.008	2.27
<i>Habitat diversity at the plot scale</i>	1.387	0.633	2.19
<i>Woodland cover at the landscape scale</i>	-11.374	4.48	-2.54

AIC = 45.01; n = 47; ω_i = 0.24

Medium elevations (1200-1800 m)

Predictors	Estimate	SE	Z
<i>Canopy trees cover at the plot scale</i>	-0.079	0.039	-1.99
<i>Precipitation factor</i>	0.408	0.207	1.97

AIC = 55.75; n = 44; ω_i = 0.53

Predictors	Estimate	SE	Z
<i>Canopy trees cover at the plot scale</i>	-0.102	0.049	-2.09
<i>Precipitation factor</i>	0.342	0.219	1.55
<i>Medium-tall shrublands at the landscape scale</i>	15.43	11.025	1.40

AIC = 55.99; n = 44; ω_i = 0.47

High elevations (1800-2200 m)

Predictors	Estimate	SE	Z
<i>Shrubland cover at the plot scale</i>	-0.015	0.006	-2.39
<i>Rocky cover at the plot scale</i>	-0.022	0.005	-4.12
<i>Habitat diversity at the plot scale</i>	0.851	0.316	2.69

AIC = 60.08; n = 82; ω_i = 0.50

Predictors	Estimate	SE	Z
<i>Shrubland cover at the plot scale</i>	-0.016	0.006	-2.43
<i>Rocky cover at the plot scale</i>	-0.019	0.005	-3.34
<i>Habitat diversity at the plot scale</i>	0.783	0.325	2.41
<i>Rocky areas at the landscape scale</i>	-0.005	0.006	-0.77

AIC = 61.45; n = 82; ω_i = 0.25

Predictors	Estimate	SE	Z
<i>Shrubland cover at the plot scale</i>	-0.015	0.006	-2.34
<i>Rocky cover at the plot scale</i>	-0.218	0.005	-4.18
<i>Habitat diversity at the plot scale</i>	0.806	0.318	2.53
<i>Slope inclination at the plot scale</i>	-0.009	0.012	-0.75

AIC = 61.50; n = 82; ω_i = 0.25

64

65