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The altitudinal frontier in avian climate impact research

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Climate change has already had profound effects on biodiversity in a range of habitats across the globe (Parmesan & Yohe 2003), including significant impacts on the distribution, abundance, productivity and survival of a range of bird species (e.g. Crick 2004, Gregory *et al.* 2009). However, evidence for effects in certain habitats and regions, including those that may be expected to experience the most profound impacts (e.g. EEA 2010, Harris *et al.* 2011), is limited, largely due to logistical and economic constraints.

High mountains are likely to be particularly vulnerable to climate change: the rate of warming in mountains has been twice the global average (Brunetti *et al.* 2009) and increasing temperatures, higher snow lines and lower snowfall, evident over the past century, are expected to continue (EEA 2010). The biodiversity of these habitats includes many specialists and species of conservation concern that are vulnerable due to large climatic variation over small spatial scales (e.g. on average, a 100-m increase in altitude equates to a $-0.5\text{ }^{\circ}\text{C}$ change in temperature; Moser *et al.* 2010). A likely consequence of climate change in mountain regions is that vegetation zones will shift upwards, a phenomenon already widely evident in changing plant communities (e.g. Pauli *et al.* 2007) and treelines (Harsch *et al.* 2009), the latter being especially relevant to birds. This could result in the loss or increasing fragmentation and isolation of high alpine habitats.

There is evidence of altitudinal shifts in bird distributions (e.g. Pounds *et al.* 2005, Tryjanowski *et al.* 2005, Harris *et al.* 2011) but less evidence of shifts in species occurring in habitats above the treeline (Popy *et al.* 2010, Maggini *et al.* 2011), and the patterns are not universal (e.g. Archaux 2004). The evidence for altitudinal range shifts in high alpine environments (which we define here as high-altitude mountain habitats at and above the natural treeline) is therefore weak at best, although other evidence suggests that birds in high-altitude habitats may respond to climate change in several ways (Beale *et al.* 2006, Bech *et al.* 2009, Pearce-Higgins *et al.* 2010). Whilst there are some schemes that include some monitoring of high alpine bird populations (e.g. the Swiss scheme, Monitoring Häufige Brutvögel (MHB); Kéry & Schmid 2006), in comparison with avian communities in other habitats, the status and trends of high alpine bird populations are poorly known (EEA 2010), due largely to the logistical difficulties of carrying out rigorous monitoring in such challenging environments. This makes an assessment of the impacts of climate change on high alpine birds problematic, yet these are likely to be among the most vulnerable groups (EEA 2010).

There is no doubt that further research on even the basic ecology of high alpine species is needed, first to quantify current distributions, secondly to establish baselines to assess future changes and

thirdly to assess fine-scale species–habitat associations. However, there is also a need to understand better the demographic mechanisms that underpin distributions and that may therefore dictate future altitudinal shifts. Such studies could also identify those species whose alpine distributions are truly (directly or indirectly) dictated by climate as opposed to other confounding factors (e.g. changes in grazing regimes; Laiolo *et al.* 2004, Garcia *et al.* 2008). The need for an understanding of demographic mechanisms in climate change research in general (e.g. Pearce-Higgins *et al.* 2011), and in relation to upslope shifts in forested habitats (Harris *et al.* 2011), has been highlighted, but there are issues unique to high alpine environments that need to be addressed if we are to detect strong evidence for climate-induced range shifts, and to make predictions about how bird communities will respond under future climate scenarios. Our aim here is to highlight these issues for high-altitude mountain habitats.

Measures of habitat quality

Ultimately, lifetime reproductive success may be the best measure of habitat quality at relatively small scales (Van Horne 1983) but this is of course extremely difficult to estimate in any habitat. Nevertheless, assessing life-history parameters along altitudinal gradients, in addition to abundance, would give insights into the mechanisms determining bird distributions. Productivity, survival and population age structure are basic parameters in demographic studies, and although there are several examples of autecological research on high alpine species (e.g. Water Pipit *Anthus spinoletta*, Rauter *et al.* 2002; Himalayan Accentor *Prunella fulvescens*, Lu 2006; Tibetan Ground Tit *Pseudopodoces humilis*, Ke & Lu 2009; choughs *Pyrrhocorax* spp, Laiolo & Rolando 2001; White-tailed Ptarmigan *Lagopus leucura*, Martin & Wiebe 2004), few have considered variation in these demographic parameters in relation to altitude (e.g. Lu *et al.* 2009, 2010), and we are unaware of any study that has considered variation along gradients that encompass most of an alpine species' altitudinal range. Furthermore, there may well be other costs that could be considered, such as parasite and pathogen infection rates (e.g. Korpimäki *et al.* 1993, Møller 1993), which can have high prevalence in high alpine species (Janiga *et al.* 2007) and may have consequences for reproductive success (Blanco & Lemus 2010). Clearly, intensive population studies along altitudinal gradients are needed to understand demographic responses to climate change.

Source-sink effects

There are many examples of species that have shown an increase in local distribution, and/or the occupation of more habitats as the population has expanded (Newton 1998), which is underpinned by density-dependent effects (e.g. Fasce *et al.* 2011, Sebastián-González *et al.* 2011). These processes often result in a greater use of less preferred and less productive habitats by lower quality individuals (Newton 1998). Such source-sink effects may mean that a factor driving population increase in the source population results in apparent upslope movements in distribution, even though the productive part of the population does not move. It is important to identify such effects before firm conclusions can be drawn about the causes of altitudinal range shifts, particularly as they can be small relative to typical territory sizes (e.g. an average upslope shift of 29 m; Popy *et al.* 2010). Certainly, climate could underpin such effects, but there are many potential 'static' effects that could cause apparent local range shifts (e.g. urbanization, changes in grazing regimes, changes in protected area management, impact of recreation).

Detailed data on life-history parameters (see above) are needed to understand fully source-sink effects, and even then identifying true 'sinks' is difficult (Watkinson & Sutherland 1995). However, relatively simple measures, in particular those related to altitudinal range boundaries (Shoo *et al.* 2006), may provide sufficient evidence to detect genuine altitudinal distribution shifts. First, precise estimation of the form of the change in distribution across a broad altitudinal gradient, following the

methods of Maggini *et al.* (2011), would provide evidence of a true shift in the mean distribution of species, as opposed to assessments of a distribution where the range expands but the mean remains static (as would be expected if source-sink effects alone are operating). Secondly, determining population age structure (e.g. through ringing) may give an insight into which are the less preferred habitats, as they typically have a higher proportion of younger (hence competitively inferior) individuals (Newton 1998).

Edge effects

The high alpine habitat (at least in a near-natural state) can be viewed broadly as one in which different habitats occur along an altitudinal gradient, comprising forest edge, transitional (scrub and scattered trees), grassland, bare rock, and permanent snow and ice fields. The interaction between birds and habitat edges may be important in determining distributions, in particular at the treeline. By the nature of the habitat, most birds nesting in high alpine areas do so on or near the ground. One of these species, the Skylark *Alauda arvensis*, avoids nesting near trees and other vertical structures in lowland habitats (Donald 2004) but we are unaware of studies considering such effects on any species in high alpine habitats. If the same processes occur, then the functional limit of the treeline for such species will be higher than the physical limit. This is important when making predictions of impacts of treeline shifts on high alpine avifauna because there will be less functional space than is apparent from the treeline alone. Estimates of functional edge effects can be quantified approximately by detailed study of bird distributions in relation to habitat edge, but intensive demographic studies such as thorough nest monitoring along altitudinal gradients are needed to reveal precise mechanisms. Understanding such mechanisms is particularly important when assessing potential impacts of fragmentation at high altitudes.

Soil processes and differential habitat shifts

Soils are important in providing a key trophic level in ecological food webs and are likely to be fundamental to the structure and function of ecosystems (Edwards *et al.* 2007). In alpine environments, the response of soils to climate change may be crucial. Predictions for advancement of vegetation zones, in particular natural treelines, should not assume that soil conditions will develop in tandem, as soil evolution, in particular in the unique conditions in high mountains, may be a long-term process. For example, in the Alps the formation of a stable and homogeneous substrata is estimated to require more than 200 years at an elevation of 2000 m asl (Freppaz *et al.* 2010). Furthermore, there is no reason to suppose that soil responses to climate change will be similar across different altitudinal zones. In particular, snow has an insulating effect on soils in winter, so decreased snow cover due to higher temperatures may lead to colder soils and have subsequent negative impacts on soil processes (Edwards *et al.* 2007). Topography is a further important factor (Freppaz *et al.* 2010), so soil formation may be similarly limited where higher elevations are composed of very steep terrain. A situation whereby treelines are advancing at lower altitudes, but where there is no concomitant response at the limit of the grassland zone, would result in a 'squeeze' in suitable habitat for open grassland species, which could be exacerbated by edge effects (see above). Soil development rates at higher altitudes may be crucial to the ability of some species to make elevational shifts in distribution, although these rates remain uncertain due to complex interactions between soil-forming processes, vegetation and, as a consequence, the availability of soil-dwelling invertebrates (von dem Bussche *et al.* 2008).

Evidence, largely from agricultural habitats, suggests that soil conditions affect birds' prey availability (e.g. Schaub *et al.* 2010), foraging success (Török & Ludvig 1988), geographical distribution (Wilson *et al.* 2002) and productivity (Pearce-Higgins *et al.* 2010). For species for which soil organisms are important prey, intensive studies to research key linkages are required.

Hypogeal organisms such as earthworms or tipulid larvae may be especially relevant, although it seems likely that soil responses to climate change may also be important for epigeal arthropods (e.g. Hosoda 1999).

Direct altitudinal effects

Environmental conditions also change along an altitudinal gradient due to factors linked to altitude *per se*, rather than to climate or anthropogenic influences, e.g. UV radiation, atmospheric pressure and oxygen levels (Martin 2001). Whether these factors are likely to limit bird species distributions within their current elevational ranges, or even within potential future ranges, seems unlikely for those species that are able to breed at very high altitudes in some parts of their range (e.g. Gldenstt's Redstart *Phoenicurus erythrogaster* 5000 m, Cramp 1988; Alpine Chough *Pyrrhocorax graculus* 5000 m, and observed foraging at 8100 m, Cramp & Perrins 1994; Snow Finch *Montifringilla nivalis* 5300 m, Cramp & Perrins 1994), suggesting there may be considerable scope for altitudinal range shifts. However, such species typically show adaptations to high altitudes, which can be both intra- and inter-specific. For example, Lu *et al.* (2009) found that snowfinches *Montifringilla* spp. at higher altitudes had longer wings, which they considered to be an adaptation to lower air density, although adaptation to strong winds may also be a driver of morphological adaptation (Martin 2001). Some species also show very high blood oxygen affinity (e.g. Andean Goose *Chloephaga melanoptera*, Jessen *et al.* 1991; White-tailed Ptarmigan, Martin 2001). It is therefore important to consider that a necessity to adapt may be an impediment to colonization of higher altitudes regardless of climatic changes. Furthermore, key resources could be limited by altitude-dependent factors, which, for example, can be important determinants of invertebrate distributions in high alpine habitats (Hodkinson 2005). Combined effects of climate change and direct effects of altitude could therefore result in a scenario of loss of habitat due to vegetation shifts at lower altitudes, but no opportunity to colonize higher altitudes due to climate-independent constraints. Studies of direct effects of altitude-dependent effects are therefore needed to identify key limiting factors for birds and their resources at high altitudes.

Monitoring at high altitude

Although we have raised a number of issues that suggest that knowledge of numbers alone may not be sufficient to detect altitudinal shifts, let alone identify the mechanisms, we believe that there is still a fundamental need to improve the monitoring of bird populations in high alpine habitats. Currently, our knowledge of changes over time is largely restricted to site-specific (e.g. Archaux 2004, Popy *et al.* 2010) or, rarely, country-specific (Maggini *et al.* 2011) studies. For most high alpine habitats globally, even basic information on variation in bird occurrence across altitudinal gradients is lacking, yet this information is vital as a precursor to the kinds of more intensive studies that we have outlined in this article. Furthermore, there are a number of pressures on the alpine environment (EEA 2010), some of which are largely independent of climate (e.g. abandonment of grazing; Laiolo *et al.* 2004, Garcia *et al.* 2008) and some of which are likely to interact with climate change, such as the effects of winter outdoor recreation (on-piste skiing, snowshoeing, back-country skiing, snowboarding, free-riding, etc.), which has demonstrated negative effects on several bird species (Arlettaz *et al.* 2007, Rolando *et al.* 2007, Braunisch *et al.* 2011, Thiel *et al.* 2011, Caprio *et al.* in press) and which is likely to become more widespread at higher altitudes as temperatures rise and snow cover reduces at lower levels (Elsasser & Messerli 2001, Scott *et al.* 2008).

Altitudinal gradients provide a good basis for studying climate change (Shoo *et al.* 2006), as the climatic conditions vary over a small spatial scale, reducing macroecological influences that may complicate the interpretation of latitudinal studies (Rahbek 2005). We suggest that it is vital to establish long-term monitoring programmes across a relatively broad area (a minimum of an entire

mountain range) that could act as a baseline to monitor altitudinal shifts in bird communities in response to climate change, and environmental change more broadly. This could be based on existing schemes (e.g. the MHB), or it could adopt a novel approach, such as point counts along altitudinal transects, but with sampling across a broad geographical area, rather than a sample limited to geo-political boundaries. Such an international programme, covering several continents, is in place for alpine plants (GLORIA; Pauli *et al.* 2007), but we are unaware of a similar programme for birds. Crucially, this would act as a springboard for the further, more intensive, studies that are necessary to predict future impacts of, and therefore make provision for, likely consequences of climate change on high alpine birds.

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