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Past and future impact of climate change on foraging habitat suitability in a high-alpine bird species: Management options to buffer against global warming effects

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ABSTRACT

The majority of predictions about the impacts of climate change on wildlife have relied either on the study of species' physiological tolerance or on broad-scale distribution models. In comparison, little attention has been paid to species' mechanistic responses to fine-grained, climate-induced modifications of habitat suitability. However, such studies would be pivotal to the understanding of species' ecological requirements (and hence their adaptive potential to environmental change) and the design of management strategies. We investigated foraging microhabitat selection in a potentially climate-change sensitive species, the white-winged snowfinch *Montifringilla nivalis*, during the breeding season in the Alps. Our microhabitat selection model considered topography, ground-cover variables and sward height within a 5-m radius at foraging and control locations. Habitat selection was positively affected by grassland cover, negatively by sward height and quadratically by snow cover (optimum around 40%); birds avoided anthropized (urban areas, roads) sites. We estimated past (1976) and future (2066) climate-driven changes in foraging microhabitat suitability, assuming a progressively earlier date of snowmelt due to increasing temperatures over this entire time span. We then modelled the potential impact of snowmelt (and related sward height) on habitat suitability under two scenarios: maintaining the current situation (i.e. irregular seasonal grazing) and implementing targeted management in an attempt to mitigate impacts of earlier snowmelt. Predicted foraging habitat suitability (estimated as the fraction of suitable plots) significantly declined over time (−23% between 1976 and 2016, further 32% loss by 2066). However, model outputs demonstrated that maintaining sward height below 6 cm on breeding grounds (e.g. by regular grazing) would significantly decrease the predicted loss of suitable foraging habitat. Detailed information about patterns of resource exploitation allows the identification of mechanistic, functional responses of species to environmental change, and enables an evaluation of habitat management options that can buffer against the detrimental effects of global warming.

1. Introduction

Anthropogenic climate change is increasingly threatening ecosystems and species worldwide (IPCC, 2013; Rosenzweig et al., 2008). Evidence from a wide range of taxa and ecological systems suggests that climate change has already started to affect biodiversity at a global scale (e.g. Carnaval and Moritz, 2008), for instance by modifying species distributions, altering their habitats or increasing extinction risk

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due to rapid shifts in abiotic conditions (Chen et al., 2011; Parmesan and Yohe, 2003). Based on forecast climatic scenarios, several studies have furthermore attempted to predict future climatic impacts on biodiversity (e.g. Bellard et al., 2012; Thomas et al., 2004).

The potential effects of climate, and hence of climate change, on animal species have been mostly assessed either by experimental approaches evaluating physiological tolerance to climate variations (e.g. temperature) at the individual level (Johnson, 1968) and under controlled environments (Chapin et al., 1995), or via large-scale distribution models, the latter representing one of the commonest ways to explore potential changes in species distributions owing to climate change (Fitzpatrick and Hargrove, 2009; Hijmans and Graham, 2006). Ecophysiological investigations usually include field observations and laboratory measurements that aim to detect how alterations of environmental constraints influence species' physiological responses and hence population processes (Arlettaz et al., 2000; Pörtner and Knust, 2007). In contrast, correlative models of species distribution (Guisan and Thuiller, 2005) rely on environmental factors such as climate, landcover and topographic variables, which are usually linked with species occurrence at a broad scale, and thus can help to identify those species that are most likely to be affected by climate or environmental change in a given area. They can, to some extent, be downscaled to the territory/home-range size of a target species (Brambilla et al., 2015; Braunisch et al., 2013), but often remain fairly limited in their predictive power as they may miss essential mechanistic components (Williams and Jackson, 2007) linked to patterns of resource exploitation, such as food acquisition. Hence, species distribution models may not embrace species' niche complexity as a whole (Braunisch et al., 2013) and may both over- and underestimate extinction risk due to climate change (Bellard et al., 2012). Although species distribution models are indeed the most widely used (and scalable) approach to assess species' spatio-temporal responses to climate change (Engler et al., 2017; Moritz and Agudo, 2013), there is a need for complementary approaches that integrate finer-scale ecological information for, on the one hand, improving our mechanistic understanding of the tolerance and resilience, i.e. the adaptive potential of target organisms to shifting environmental conditions (e.g. Baudier et al., 2015; Bennett et al., 2015), and, on the other hand, modelling appropriately the consequences of environmental changes upon population dynamics (Fedy and Martin, 2011; Fordham et al., 2017). This could be addressed by considering the impacts of climate change upon fine-scale habitat structure and availability (henceforth, microhabitat), which eventually drives habitat suitability. However, this aspect has received comparatively little attention so far, despite its crucial importance in understanding mechanistic responses of species to environmental change (Fordham et al., 2017; Kearney and Porter, 2009). Fine-grained species-habitat associations are essential to understand how changes in microhabitat due to climate change will affect species' habitat suitability at local and broader scales, which will ultimately influence a species' ability to respond to climate-induced environmental changes (Scheffers et al., 2014).

Studies of the effects of microhabitat alteration due to changing climatic conditions have mostly focused on small-sized organisms (e.g. invertebrates) that are highly sensitive to local climatic/habitat variation, especially due to their strong temperature-dependent life-cycles (Davies et al., 2006). Pincebourde et al. (2016) have shown that microhabitat properties shape species responses to climate change. Research has generally focused on species with limited mobility (e.g. plants (Pradervand et al., 2014), benthic invertebrates (Schiel et al., 2004)). In contrast, studies on the distribution of terrestrial and highly-mobile species usually deal with broad spatial scales, despite the fact that habitat selection in these species operates at multiple scales. In birds for instance, this concerns the selection of breeding sites (Jedlikowski et al., 2016; Rauter et al., 2002), foraging grounds (Brambilla et al., 2017b; Martínez-Miranzo et al., 2016; Schaub et al., 2010), and even shelters to avoid unsuitable climate (Visinoni et al., 2015). An absence of information about microhabitat preferences can lead to serious biases in predictions of climate change effects on species' distributions (cf. Bellard et al., 2012). As a matter of fact, microhabitat characteristics may allow species persistence when the general climate of the region appears to have become unsuitable, and vice versa. Studies of microhabitat suitability are thus pivotal to our basic understanding of species' ecological requirements and to devise efficient conservation management of climate-sensitive biodiversity. Several such studies have emerged recently (Suggitt et al., 2011; Turlure et al., 2010), which have established the importance of both microhabitat and microclimate to understand the sensitivity of species to environmental shifts and, ultimately, their population dynamics and distribution patterns (Fedy and Martin, 2011; Frey et al., 2016). The basic question here can thus be formulated as follows: to which extent can microhabitat characteristics, and their potential management, buffer against any detrimental effects of overall climate change (e.g. Braunisch et al., 2014)?

Among terrestrial organisms, high-elevation cold-adapted species seem to be particularly vulnerable to climate change (Dirnböck et al., 2011; Lagerholm et al., 2017; Scridel et al., 2018), with their future distribution being either expected to contract towards higher elevations due to ambient temperature warming (Braunisch et al., 2013; Chamberlain et al., 2013; La Sorte and Jetz, 2010; Pernollet et al., 2015; Sekercioglu et al., 2008), or to vary in a complex way in response to shifts in precipitation regimes that remain difficult to forecast (e.g. Tingley et al., 2012). Mountain areas are indeed subject to higher rates of warming compared to the global average (e.g. Böhm et al., 2001; Brunetti et al., 2009), yet at the same time, they are also experiencing strong changes in landscape and land use (e.g. forest encroachment in abandoned pastures, upward treeline shift or loss of areas permanently covered by snow). High-elevation ecosystems thus represent an ideal setting to investigate the fine-grained impact of environmental change on habitat and biocenoses, especially due to the complex topography, including steep elevational gradients, that generates a large range of microhabitats and microclimates (hereafter topoclimates) and offers numerous refugia opportunities (Körner and Ohsawa, 2006). Such heterogeneity may per se represent a chance to maintain biodiversity, either naturally (Brambilla et al., 2016) or through informed conservation management (Braunisch et al., 2014). However, to the best of our knowledge, mitigation strategies to maintain niche opportunities for high-alpine biodiversity facing climatic risks have not been investigated so far (Shoo et al., 2011; Turlure et al., 2010).

In this study, we investigated the foraging microhabitat selection in a high-elevation, cold-adapted and snow-exploiting passerine bird, the white-winged snowfinch *Montifringilla nivalis* (Aves: Passeridae; henceforth: snowfinch), during the nestling rearing period, a crucial phase of the life-cycle. The snowfinch is a mountain specialist species breeding at high elevations above the treeline (in the European Alps mostly between 1800 and 3000 m asl; Cramp and Perrins, 1994). Nests are usually located in rock crevices or human-built infrastructure such as mountain buildings or ski-lift pylons (Cramp and Perrins, 1994). Females lay the first clutches of 4–5 eggs during the second half of May to early June, and nestlings fledge at ca.18–22 days of age (del Hoyo et al., 2009). During the nestling rearing period, adults collect invertebrate prey in the surroundings of nest sites, usually within 300 m of the nest, frequently on or at the margin of melting snow patches and in alpine grasslands (Antor, 1995; Brambilla et al., 2017b; Catzeflis, 1975; Cramp and Perrins, 1994; Strinella et al., 2007).

A recent study of foraging habitat selection by breeding snowfinches in the Italian Alps highlighted the importance of habitat factors that are largely climate-dependent, such as snow cover (positively selected), height of the grass sward (lower sward preferred), and solar radiation (lower values favoured, especially late in the season, indicating avoidance of warmer sites). This previous study was based on 314 m^2 plots (i.e. at a meso-scale) and did not explicitly address the key question of climate change effects on habitat suitability (Brambilla