Conserving temperate montane birds under climate change: an assessment of potential management options

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Abstract

Montane species are particularly vulnerable to the threats posed by climate change. As temperatures increase, their climatic niche will shift upwards – and species must either adapt to warmer conditions, or migrate to avoid extinction. In the first section of this thesis, I assessed the feasibility of management strategies available to conservation practitioners for conserving montane bird species under climate change. I integrated the dimensions of vulnerability outlined in previous research with management strategies relevant to the conservation of montane birds in order to specify the most appropriate strategy for species that display certain elements of vulnerability. I also outline the specific data and research needs that would allow conservation practitioners to more rigorously assess the management strategy for their focal montane species.

It is evident that for some highly specialised species – such as alpine birds that are restricted to habitats above the treeline – conservation practitioners will be more limited in their choice of management approach. Assisted colonisation (AC) has been proposed as a strategy for mountaintop species with nowhere left to go. However, this strategy is reliant on the identification of suitable sites elsewhere. In the second section of this thesis, I focused on the identification and assessment of potential AC sites for European alpine birds. My results highlight the severe threat posed by climate change, with European alpine birds projected to lose 57-80% of their climatically suitable area by 2080. I identified promising AC sites that will sustain suitable conditions under climate change for the majority of species considered. My findings are useful for guiding conservation practitioners to the most suitable AC sites for alpine birds under climate change, as well as for identifying the most suitable source populations for translocating individuals to those sites, the latter of which represents a novel approach.

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AC	Assisted colonisation
AMK	Group of mountains in the countries of Albania, Moldova and Kosovo.
AUC	Area under the curve (evaluation metric)
BMG	Group of mountains in the countries of Bulgaria, Macedonia and Greece.
EEA	European Environment Agency
GBIF	Global Biodiversity Information Facility
GCM	General circulation model
GHG	Greenhouse gas
GMBA	Global mountain biodiversity assessment
IPCC	Intergovernmental Panel on Climate Change
IUCN	International Union for Conservation of Nature
LC	Least Concern (conservation status)
PA	Protected area
PCA	Principal components analysis
RCM	Regional circulation model
SDM	Species distribution model
SRES	Special Report on Emissions Scenarios
TGF	Targeted gene flow
TSS	True skill statistic (evaluation metric)
VU	Vulnerable (conservation status)

Chapter 1

Introduction

1.1 Introduction to the thesis

Climate change threats to biodiversity

The average global surface temperatures increased by 0.85°C during the period between 1880 and 2012 (IPCC 2014). There is substantial evidence that global climatic change cannot be entirely explained by natural variation, but is instead as a result of anthropogenic actions, such as the increase in greenhouse gas (GHG) emissions to levels that are the highest in history (IPCC 2014). According to modelled projections, mean global surface temperatures are expected to increase at an accelerated rate, potentially exceeding 4°C by 2100 depending on future GHG emissions and the responses of human society (IPCC 2014).

The responses of species and communities to climate change are diverse and complex. Some species have already responded by changing their phenological events (e.g. time of flowering in plants; Szabó *et al.* 2016), altering their biotic interactions (Tylianakis *et al.* 2008) and shifting their distributions (Chen *et al.* 2011). However, the documentation of true evolutionary processes, where a species has become more adapted to altered conditions through changes in its genetic composition, is rare (Merilä & Hendry 2014). Climate change is likely to overwhelm the adaptive capacity of many species, advancing too rapidly for evolutionary adaptation to take place (Quintero & Wiens 2013). Only a limited proportion of species will possess the traits required to adapt *in situ* to changing environmental conditions (Foden *et al.* 2013), while the majority will have to shift their distributions in the direction of suitable climate, or face extinction. General warming trends indicate that species distributions will be forced polewards and upwards in elevation as their climatic niches shift (Loarie *et al.* 2009). It is expected that not all species will be able to keep up with their shifting climatic niche due to intrinsic dispersal limitations and both natural and anthropogenic barriers to dispersal (e.g. mountains, water bodies and urban landscapes) (Walther *et al.* 2002; McLachlan *et al.* 2005; Schloss *et al.* 2012). For some highly specialised species, the conditions of which they require to survive may disappear entirely.

Climate change impacts on birds

The aforementioned species responses to climate change (changes to phenology, biotic interactions and distribution) have each been documented in birds. For example, the timing of spring migration has been advancing for many bird species in order to coincide with increases in spring temperature (Hurlbert & Liang 2012), which has also caused some species to breed sooner

(Møller *et al.* 2010). However, shifts in the timing of breeding events have caused the uncoupling in the synchrony of breeding and food supply for some bird populations (Van der Jeugd *et al.* 2009). One of the most commonly reported responses has been the poleward shifts in species' northerly range margins, with evidence stemming from the United Kingdom (Gillings *et al.* 2015), Finland (Virkkala & Lehikoinen 2014), France (Devictor *et al.* 2008) and across the European continent (Maclean *et al.* 2008). Similar findings have also been reported in North America, with southerly distributed birds having shifted their distributions northwards at an average rate of 2.35 km/year (Hitch & Leberg 2007). In addition to poleward shifts, species distributions have also undergone elevational shifts (e.g. Archaux 2004; Tingley *et al.* 2009; Maggini *et al.* 2011). The general expectation is that species will shift their distributions upslope with rising temperatures (Archaux 2004), but research has shown that shifts are varying in terms of both direction and magnitude, depending on the species and region (e.g. Maggini *et al.* 2011; Tingley *et al.* 2012, see Figure 1.1 for causes of distribution shifts in montane bird species). However, for many species, distribution shifts are lagging behind the shifting climate (e.g. Devictor *et al.* 2008), indicating that the climate is changing faster than the rate at which species can respond.

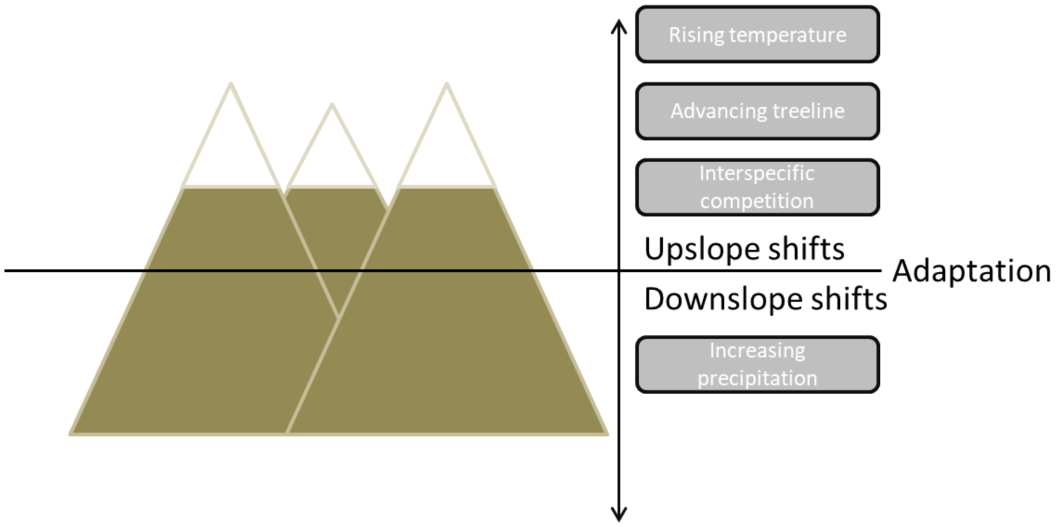

Figure 1.1. Processes influencing the directional shifts of montane birds under climate change. Montane species are likely to track their thermal niches upslope as temperatures will become less favourable at lower elevations and more favourable at higher elevations (Freeman & Freeman 2014). Advancing treelines will reduce suitable habitat for alpine species and facilitate upslope shifts for subalpine and forest-dwelling montane species (Ferrarini *et al.* 2017). The increased presence of novel competitors at lower elevations is likely to induce upslope shifts for some montane species (Jankowski *et al.* 2010). Precipitation has a direct impact on the population growth and the survival rate of birds, and recent increases in montane regions have caused downslope shifts in some montane species (Tingley *et al.* 2012).

Modelling species distributions

Species distribution modelling (SDM), also referred to as bioclimatic envelope modelling or ecological niche modelling (depending on the variables), is the process of determining environmental predictors of species distributions and projecting the optimal combination of these predictors through space (Guisan & Thuiller 2005). SDMs are increasingly used to forecast species' responses to climate change (e.g. Huntley *et al.* 2008; Barbet-massin *et al.* 2012; Thuiller *et al.* 2014). The assumption is that if SDMs can reliably predict the current distribution of a species based on current climatic conditions, they will also be able to reliably predict the future distribution of a species based on projected future climate. These distribution projections can be used to assist conservation planning and decision making under climate change, by identifying locations for future conservation reserves (Kremen *et al.* 2008), managing potential biological invasions (Guisan *et al.* 2013) and identifying suitable sites for a translocation attempt (Hoegh-guldberg *et al.* 2008). The successful range shift and population change predictions made by SDMs (e.g. Araujo *et al*. 2005; Gregory *et al.* 2009) highlights their usefulness to conservation practitioners who wish to increase the adaptiveness of species and ecosystems to the ongoing and future effects of climate change.

Management

In the past, the general conservation strategy has been to maintain species within local protected areas and fixed-boundary reserves. However, climate change threatens this strategy as most species are unlikely to remain stationary whilst their climatic niches shift (e.g. Hole *et al.* 2009; Araujo *et al.* 2011; Bagchi *et al.* 2013). Dynamic protected area management plans that focus on resilience-based adaptation strategies with the aim of facilitating shifting distributions have been proposed (Mawdsley *et al.* 2009; Poiani *et al.* 2011). However, even these adaptive strategies may not suffice in the fight to prevent some species and populations, such as those restricted to mountain tops, from climate-induced extinction. Under these circumstances, conservation practitioners may be forced to explore alternative management strategies such as assisted colonisation (Hoegh-guldberg *et al.* 2008), which involves the human-mediated movement of taxa beyond their indigenous range to suitable habitats elsewhere (an assessment of this strategy and other alternative management strategies is provided in Chapter 2).

Thesis outline

This thesis focuses on the conservation of temperate montane avifauna under the effects of climate change. As evidence begins to emerge of the population declines of montane birds as a result of climate change (Lehikoinen *et al.* 2014; Flousek *et al.* 2015), it is important to assess the potential management options available to conservation practitioners for conserving these species.

The following chapters begin with a review of the literature, focusing on an assessment of different management strategies (e.g. protected area management, connectivity, assisted colonisation and targeted gene flow) available to conservation practitioners for conserving montane birds. Following on from this, the future suitable climate of European alpine birds is modelled and the model outputs are used to assess assisted colonisation, a conservation technique regularly cited for species restricted to the highest altitudes (e.g. Hoegh-guldberg *et al.* 2008; Loss *et al.* 2011; Thomas 2011), as a management technique for their conservation. Sourcing individuals from populations that are best adapted to conditions at a potential assisted colonisation site is recommended in the International Union for Conservation of Nature (IUCN) Guidelines for Reintroductions and Other Conservation Translocations (2013). However, there is no clear method that specifically addresses the identification of candidate source populations. Therefore, a novel approach is presented that aims to overcome this deficiency. In the final section of the thesis, a discussion of the key findings emerging from each of the distinct chapters is presented and areas for future work are recommended.

1.2 Aims of the thesis

The overarching goal of this research is to assess the management strategies available to conservation practitioners for conserving montane bird species under climate change. This research will address the following questions and aims:

Q1. How can traditional and alternative management strategies be used for conserving montane birds under climate change?

- ***Aim 1a***. Assess the feasibility of traditional and alternative management strategies for conserving temperate montane bird species.
- ***Aim 1b.*** Identify data and knowledge gaps that if filled, would provide conservation practitioners with the evidence and information to better assess the most suitable strategy for their focal species.

Q2. Are there suitable sites beyond the dispersal capability of alpine birds in Europe that could be used as recipient localities for assisted colonisation?

- ***Aim 2a.*** Predict the future distributions of European alpine bird species under climate change.
- ***Aim 2b.*** Identify potential assisted colonisation sites beyond the dispersal capability of those species.

- ***Aim 2c.*** Assess potential assisted colonisation sites in terms of habitat suitability and protected area coverage.

Q3. How can a candidate source population be identified for an assisted colonisation attempt?

- ***Aim 3a.*** Identify the most climatically suitable source population for each potential assisted colonisation site using principal components analysis.

Chapter 2

Limited distributions, limited options: assessing the feasibility of alternative conservation actions for temperate montane birds

Abstract

Temperate montane bird populations are declining as a result of climate change. These species are faced with a situation in which they must adapt to warmer conditions within their current ranges, or shift their ranges further upslope in order to maintain their climatic optimum. However, upslope shifts will leave them with less habitable area due to the finite amount of space available as they approach mountain peaks. I reviewed the literature in order to assess the feasibility of different management strategies for conserving temperate montane birds under climate change. Even within this relatively specialised group of species, determining the most appropriate management strategy will be highly variable. Conservation practitioners should begin by identifying the characteristics of their focal species' vulnerability under climate change (e.g. exposure, sensitivity and adaptive capacity). I identify the most appropriate management strategy for species that exhibit certain combinations of vulnerability under climate change. I also address the key action and research required for conservation practitioners to more rigorously assess the vulnerability and choice of management strategy for montane species under climate change.

2.1 Introduction

Climate change is recognised as posing a significant threat to biodiversity worldwide (Thomas *et al.* 2004; Bellard *et al*. 2012). Species are responding to climate change in a range of ways, including by shifting their distributions (Chen *et al.* 2011), altering their phenological events (Walther *et al.* 2002) and changing their biotic interactions (Blois *et al.* 2013). Many species have shifted their distributions poleward and upward in elevation over the last century (Root *et al.* 2003; Tingley *et al.* 2009; Maggini *et al.* 2011). These shifts are projected to accelerate under future climate change, leaving some species with less habitable area (Barbet-massin *et al.* 2012). The impact of climate change is thought to be particularly great for montane species, which are often range-restricted and show high levels of endemism (Brooks *et al.* 2006; Sekercioglu *et al.* 2008; La Sorte & Jetz 2010). The already-limited distributions of these species, coupled with the finite amount of space available in mountains for tracking their climatic niches, makes them especially susceptible to decreases in range size. Due to the typically strong link between population sizes and range sizes (Purvis *et al.* 2000), these retracting distributions are likely to cause population declines and extinctions.

Throughout temperate montane systems, evidence of range retractions and population declines are already being linked to the changing climate (Inouye 2008; Lehikoinen *et al.* 2014; Tayleur *et al.* 2016). Traditional biodiversity management strategies that aim to protect specific species assemblages within protected areas may lose their effectiveness under climate change (Araujo *et al.* 2004; Hannah *et al.* 2007). As species shift their distributions in response to the changing climate, many individual protected areas will experience substantial turnover in faunal composition (Araujo *et al.* 2011; Bagchi *et al.* 2013). Distribution shifts will leave some species with less representation in protected area networks that were originally designed to conserve them (Hole *et al.* 2009). Therefore, those responsible for the conservation of vulnerable montane species may be forced to explore more flexible management strategies that acknowledge the dynamic nature of climate change. Strategies such as assisted colonisation and targeted gene flow are two such examples that have gained considerable traction over the past decade (Hoegh-guldberg *et al.* 2008; Hewitt *et al.* 2011; Weeks *et al.* 2011; Aitken & Whitlock 2013). Montane species are potentially ideal candidates for these alternative management approaches because they have a limited capacity to adapt *in situ* to advancing climate change (Hoegh-guldberg *et al.* 2008; La Sorte & Jetz 2010). However, both management strategies have a number of potential risks attached (Hewitt *et al.* 2011; Weeks *et al.* 2011), and this has attracted criticism from scientists who argue that in many cases these risks outweigh the potential benefits (e.g. Ricciardi & Simberloff 2009a; b). This leaves conservation practitioners in a difficult position as they try to evaluate the most appropriate management strategy for the species under their responsibility.

Here, I explore the methods available to conservation practitioners for predicting future changes to montane bird distributions, identify the implications of these distribution changes and assess the feasibility of traditional and alternative management strategies relevant to conserving temperate montane birds under climate change. The focal taxa of this review are bird species and subspecies with breeding distributions restricted to temperate mountainous environments throughout their entire range. Potentially due to the logistical challenges of biodiversity monitoring in harsh and inaccessible environments, this vulnerable group has received relatively little research attention, even in well-studied regions such as Europe (EEA 2010; Chamberlain *et al.* 2012). In recognition of this, I also aim to identify the key data and knowledge gaps that if filled, would provide conservation practitioners with the evidence and information to better assess the most suitable strategy for their focal species.

2.2 Climate change effects and montane bird responses

Recent population declines in temperate montane bird populations have been linked to climate change (Lehikoinen *et al.* 2014; Flousek *et al.* 2015). As climate change advances, the effects of shifting vegetation zones (e.g. Pauli *et al.* 2007; Ferrarini *et al.* 2017) and physiological stresses imposed by novel climatic conditions (e.g. Jiguet *et al.* 2010; Oswald & Arnold 2012) will become more pronounced within species current ranges. In response to these changes, montane species have typically shifted their ranges towards higher altitudes (e.g. Popy *et al.* 2010; Maggini *et al.* 2011; Flousek *et al.* 2015), though evidence suggests that for many species, distribution shifts are lagging behind climate shifts (Devictor *et al.* 2008; Forero-Medina *et al.* 2011; Chen *et al.* 2011). For montane species that track their climatic niche, the finite amount of space available in mountains for upslope shifts will ultimately leave them with smaller range sizes, which consistently emerges as a key correlate of increasing extinction risk in birds (Lee & Jetz 2011). In some extreme cases, the climatic niche of species and populations are projected to shift beyond the peaks of mountains (Sekercioglu *et al.* 2008), potentially forcing them to adapt or become extinct.

Species range shifts under climate change will result in altered interactions and novel assemblages (Blois *et al.* 2013). Warming in mountain systems will favour the colonisation of warm-adapted species previously confined to lowlands (e.g. Wilson *et al.* 2007; Moritz *et al.* 2008; Pauli *et al.* 2012). Some of these warm adapted species will present new threats in the form of competition or predation, potentially at the expense of native montane species. Evolutionary theory suggests that the higher margin of a species elevational range is mediated by stress-related abiotic mechanisms while the lower margin is mediated by competition (MacArthur 1972; Connell 1978). Therefore, an increase in competition at montane species' lower range boundaries is likely to lead to both range size and population size decreases. Recent transplant experiments of montane plant communities that emulated a failure to track climate change showed that their performance was strongly reduced by novel competitors which could migrate upwards from lower elevations (Alexander *et al.* 2015). Increases in interspecific competition at lower range boundaries through asymmetric aggression (e.g. Jankowski *et al.* 2010) or competition for valuable resources (e.g. nesting cavities, Harris & Siefferman 2014) could drive montane bird species further towards mountain peaks (Jankowski *et al.* 2010).

The phenologies of bird species and of the taxa' with which they interact are changing (Visser *et al.* 2012). In many cases these changes are not in unison, thus creating mismatches in the timing of annual cycle events (Visser *et al.* 2012). For example, the timing of breeding for birds may become desynchronised from the time when food is most abundant or available at all (e.g. Both *et al.* 2006). Research on migratory birds found that declining species did not advance their spring migration, whereas those with stable or increasing populations advanced their migration considerably (Møller *et al.* 2008). The effects of phenological changes for montane bird species are not as well documented as those for their lowland counterparts. Nonetheless, specialists that depend on particular resources that are available for a limited period are more vulnerable than are generalists, which may be able to switch to alternatives to meet their needs as phenologies change (Miller-rushing *et al.* 2010). For example, there are a number of specialised montane bird species that forage on invertebrates in and around snow patches during the chick-rearing period (Antor 1995; Rosvold 2016; Brambilla *et al.* 2017). Climate warming is projected to affect the extent and duration of alpine snow fields in the spring and summer (Gobiet *et al.* 2014), which is likely to have consequences for montane bird populations that utilize this specialised food source (Brambilla *et al.* 2017).

2.3 Adapting to climate change

Some species may have the adaptive capacity to persist within their current distributions or disperse to more suitable regions elsewhere as climate change advances (Dawson *et al.* 2011). The adaptive capacity of a species or population is dependent on a variety of intrinsic factors, including genetic diversity, phenotypic plasticity, life history and dispersal ability (Foden *et al.* 2013). The general assumption is that montane birds will adapt to climate change by shifting their distributions in the direction of suitable climates, which is widely supported in the literature (e.g. Parmesan *et al.* 1999; Hickling *et al.* 2006; Chen *et al.* 2011). However, for high altitude species that are already approaching mountain peaks, upslope distribution shifts would no longer be an option, therefore, they would be required to disperse to suitable mountains that reach higher altitudes or closer to the poles. Due to the often-fragmented and isolated orientation of mountain topography within the wider landscape, existing and future suitable climates are likely to be separated by areas of lowland habitat (e.g. Hilbert *et al.* 2004), which is fundamentally unsuitable for montane species. Under these circumstances, adaptation through means of dispersal seems improbable. The alternative is to remain *in situ* under impending climate change. Research in the French Alps which involved a repeated count survey in the 1970s and the 2000s failed to find upslope distribution shifts for the majority of species, despite a 2.3°C increase in spring temperatures between the two periods (Archaux 2004). If populations of those species that did not shift their distributions over the two periods remained stable (or increased), then perhaps there are adaptive mechanisms at play (but see Merilä & Hendry 2014 for the many pitfalls of attempting to infer adaptation under climate change). However, it is doubtful that specialised montane birds, with requirements for habitats that are projected to be rapidly altered by the changing climate (e.g. alpine meadows), will possess the adaptive capacity for persisting in novel habitat types (e.g. forests).

2.4 Predicting climate change impacts for conservation

Species distribution models (SDMs) have the potential to assist conservation practitioners with a range of management related processes. They have been widely used to forecast the consequences of climate change for the distributions of species (Peterson 2003; Jackson *et al.* 2015; Brambilla *et al.* 2016; Tayleur *et al.* 2016), examine the efficacy of protected area networks (Hole *et al.* 2009; Araújo *et al.* 2011) and aid in conservation decision-making (Sinclair *et al.* 2010; Guisan *et al.* 2013; Meller *et al.* 2014). In most cases, SDMs are correlative, requiring only occurrence data and information on the environment at the occurrence localities to produce spatially explicit predictions of habitat suitability. However, by excluding many of the processes and biotic interactions that regulate species distribution dynamics, correlative models run the risk of producing erroneous predictions of future species distributions (Vallecillo *et al.* 2009). Additional data on the distributions, habitat preferences, and biotic interactions of species could considerably improve these models, but obtaining such data can be labour intensive and in many cases unfeasible. Mechanistic models offer a more detailed alternative to correlative models, as they evaluate the bio-physiological traits of a species to establish the conditions required for it to persist, using observations made in a controlled field or laboratory setting (Kearney & Porter 2009). However, the substantial data requirements of this approach make it less viable for rare or data-deficient species, which often represent those most at risk from extinction (e.g. range-restricted species, especially those on mountain tops; La Sorte & Jetz 2010). This is particularly the case for mountainous species, where the status and trends of bird populations are poorly known compared to those in other habitats (EEA 2010).

Key considerations for modelling montane species

An important consideration when modelling species distributions is the resolution (scale) of the gridded environmental layers (Guisan *et al.* 2007). The choice of resolution may be largely dependent on the size of the study area, or the type of ecological question under contemplation. In the context of montane species, the effect of resolution choice becomes more pronounced as the temperature in mountain environments can vary by several degrees across just a few meters (Scherrer *et al.* 2011). This means that coarse resolution continent-scale climate models may overlook the presence of locally adapted ecotypes across montane species' ranges, and run the risk of overestimating the ability of local populations to adapt to climate change (Trivedi *et al.* 2008). However, environmental and species data at continental scales tend to be at coarse resolutions due to the difficulty and expense of data sampling over large areas.

The spatial distribution of a species is dependent on habitat availability and dispersal capability.

Therefore, suitable habitats situated beyond the dispersal reach of a species are unlikely to be colonised and incorporated into a species' distribution, irrespective of their size or quality. Despite the clear importance of accounting for dispersal when predicting future species' distributions (e.g. Isaac *et al.* 2008), in most cases SDMs only consider two extreme (unlimited or none) dispersal scenarios (Bateman *et al.* 2013).This weakness is exemplified when modelling the future distributions of mountain-restricted species because of the often-fragmented and isolated orientation of mountain systems within the wider landscape. Mountains tend to be separated by extensive lowlands that contain fundamentally unsuitable habitats and climates for montane species, and SDMs that fail to consider dispersal limitations make the assumption that species will track their climatic niche through these areas to newly emerging suitable habitats. In recognition of the clear importance of accounting for dispersal in SDM projections, there are now a number of methods available for implementing 'intermediate' dispersal scenarios that use actual natal or breeding dispersal estimates to limit model projections (e.g. Engler *et al.* 2012; Barbet-massin *et al.* 2012). However, the next challenge lies in the recording of reliable dispersal estimates, which for the majority of bird species remain elusive (but see Paradis *et al.* 1998 or Martin *et al.* 2008). This is largely as a result of the difficulty associated with estimating dispersal for birds, or any taxa, as it requires either the application of expensive satellite tagging equipment (e.g. Margalida *et al.* 2013), or the analysis of ring recovery data from a sufficient number of widely distributed localities (e.g. Paradis *et al.* 1998). The latter is particularly problematic for montane species as there are a limited number of ringing groups that operate in mountain environments.

2.5 Management strategies for montane birds

Climate change presents a unique set of challenges to those responsible for the conservation of biodiversity. Unlike other threats, such as habitat destruction or hunting, where active management and intervention can in some cases restore species and ecosystems to previous states within a relatively short timeframe (Lotze *et al.* 2011), the impacts of climate change will continue long into the future and may potentially be irreversible (Meehl *et al.* 2005; Solomon *et al.* 2009). High mountains have been identified as being particularly vulnerable to the changing climate (Brunetti *et al.* 2009), as increasing temperatures, higher snow lines and lower rates of snowfall are expected to continue at an accelerated pace over the coming century (Hantel *et al.* 2000; Barnett *et al.* 2008). The consequences of these changes for the specialist bird species that rely upon these fragile mountain systems are beginning to emerge (e.g. Lehikoinen *et al.* 2014; Flousek *et al.* 2015). Those responsible for conserving these species must devise management plans that account for the fast-moving and far-reaching nature of climate change. The following sections of this review focus on a number of management strategies and their potential for conserving temperate montane birds under climate change.

Management and creation of Protected Areas

Existing protected area (PA) networks around the world have been designed to protect static (as opposed to dynamic) patterns of biodiversity (Gaston *et al.* 2006). The performance of these static PA networks is likely to deteriorate under climate change as they lack the flexibility required to maintain populations of species whose distributions shift in response to a changing climate (Hannah *et al.* 2005; Monzón *et al.* 2011; Ferro *et al.* 2014). This is not to say that PAs will not be important for montane bird conservation; there are a number of examples of species performing better inside protected areas than out (Suárez *et al.* 1993; Herremans & Herremans-Tonnoeyr 2000; Thomas & Gillingham 2015). However, they may end up supporting species communities that they were not originally intended for (Hole *et al.* 2009). For example, Araujo *et al.* 2011 suggests that PAs in mountainous regions of Europe (e.g. Alps, Pyrenees and Carpathians) will receive some of the highest numbers of 'winner' species under climate change as conditions become more favourable. The majority of these so-called 'winner' species are currently restricted to lowland and lower-montane habitats and therefore have the capacity to advance their distributions into alpine environments. In contrast, current alpine specialists have a much more limited capacity to shift their distributions, as their lower range boundaries already sit at much higher elevations. Research suggests that recently colonising bird species in the U.K. from elsewhere in Europe have disproportionately established breeding populations in PAs (Hiley *et al.* 2013). If the same were to happen in montane regions, this could cause increases in interspecific competition within PAs as colonists take advantage of the favourable conditions and compete with alpine specialists through resource exploitation or interference. These novel competitive exchanges could drive the ranges of alpine specialists further towards the mountain peaks (Jankowski 2010), potentially interacting with and exacerbating the climate-induced upslope shifts already predicted by SDM-based studies (e.g. Şekercioğlu *et al*. 2008). This exposes the limited capacity that PAs have to prevent the extinction of montane specialists with distributions that are already approaching mountain peaks.

It is important to note that not all montane specialists will be faced with a situation in which they have nowhere left to go, at least not in the immediate future. In fact, some montane species, particularly those in the higher and more expansive temperate mountain ranges of the Himalayas, the Rocky Mountains and the Alps, may still have considerable room for upslope shifts. For example, the Western Tragopan *Tragopan melanocephalus* breeds in temperate coniferous and deciduous forests in the Himalayas at an estimated elevational distribution of 2,400-3,600m

(Grimmett *et al.* 1998). The topographical shape of the Himalayas means that this species, along with other Himalayan species with similar elevational distributions, could actually experience increases in range size as they shift upslope due to the shallower inclines and plateaux's which cause increases in available area between 3,000 - 4,500m (Elsen & Tingley 2015). PAs will remain important for these species as they attempt to shift upslope and adapt to climate change, especially given the limited extent of natural or semi-natural habitats remaining outside PA networks and the continuing loss and fragmentation of unprotected sites.

In order to optimize the future effectiveness of PA networks for montane birds under climate change, conservation practitioners must employ planning frameworks that rigorously address climate-change adaptation, for example, by maximizing the ability of PA networks to facilitate uninterrupted upslope shifts in species distributions. There are now a number of frameworks and tools available to conservation practitioners for incorporating climate change adaptation strategies into the planning and management of PA networks (e.g. Hole *et al.* 2011; Cross *et al.* 2012; Stein *et al.* 2013). Furthermore, the International Union for Conservation of Nature has recently published guidelines aimed at protected area managers and planners on how best to adapt their PAs to ongoing climate change (Gross *et al.* 2016).

Maintaining and enhancing connectivity

Maintaining and enhancing connectivity – the degree to which a landscape facilitates the movement of organisms (Tischendorf & Fahrig 2000)— is regularly cited as one of the key management strategies for species conservation under climate change (e.g. Mawdsley *et al.* 2009; Heller & Zavaleta 2009; Hannah *et al.* 2014). The enhancement of connectivity between suitable habitat patches and PAs can improve the dispersal and genetic exchange of species units (e.g. Christie & Knowles 2015). For montane species like the aforementioned Blood Pheasant in the Himalayas, connectivity measures could be put in place to facilitate elevational shifts in tandem with the altering climate. Ensuring there is sufficient connectivity between PAs and suitable habitat patches that remain uninterrupted by anthropogenic development will be integral to enhancing a species' adaptive capacity. However, anthropogenic development in the form of buildings, access roads and ski-pistes threaten the connectivity of montane systems for birds and other taxa. These developments have already degraded montane habitat in parts of the Alps (Wipfe *et al.* 2005; Barni *et al.* 2007), which in turn has had a detrimental effect on the richness and density of native bird communities (Rolando *et al.* 2006; Caprio *et al.* 2011). Future climate warming will likely see an upsurge in the severity of this conflict, as increased snowlines will encourage the ski tourism industry to advance further upslope in search of sufficient snow cover

(Elsasser & Bürki 2002; Scott *et al.* 2008), thus disrupting the connectivity and degrading the habitat of alpine birds (Brambilla *et al.* 2016). Conservation strategies need to consider preventing the construction of ski-tourism infrastructure in sites of high current and potential future conservation value (e.g. alpine meadows, Brambilla *et al.* 2016) in order to avoid further impediment of montane species' prospects of adapting to climate change.

In addition to, or in replacement of climate-induced elevational shifts, the future climatic niches of some species are projected to shift vast latitudinal distances beyond their existing distributions (e.g. Hilbert *et al.* 2004) - potentially too far to be connected up. In Europe, suitable climates for two montane specialists (White-winged Snowfinch *Montifringilla nivalis* and Yellow-billed Chough *Pyrrhocorax graculus*) are projected to emerge in the Scandinavian Mountains under future climate change (Smith *et al.* 2013), an area which is more than 900km north of their current northerly range boundaries in the Alps. The expansive lowlands and impermeable matrix of anthropogenic land cover that separates these two mountain ranges make colonisation through means of natural dispersal highly unlikely. It has been proposed that connectivity strategies in the form of 'corridors' and 'stepping-stones' can improve the adaptive potential of species by linking up existing distributions with PA networks in areas that are projected to hold persistent suitability under future climate change (e.g. Heller & Zavaleta 2009; Cushman *et al.* 2013). However, this approach is unlikely to be feasible in circumstances where existing and projected future distributions are separated by areas of lowland habitat, which is fundamentally unsuitable for most montane species. Unfortunately, this unfeasibility is likely to be a common issue for species whose climatic niches shift beyond mountain peaks due to the often-fragmented and isolated orientation of mountains within the wider landscape. Therefore, alternative management techniques that can aid the colonisation of distant suitable habitat patches or increase the adaptive capacity of species within their current ranges may need to be pursued if vulnerable montane species and populations are to be prevented from extinction.

Assisted colonisation

Assisted colonisation, also referred to as 'assisted migration' or 'managed relocation', has been suggested as a conservation technique for preventing the extinction of range-restricted species that have a limited capacity to adapt *in situ* to climate change (Hoegh-guldberg *et al.* 2008; Hewitt *et al.* 2011; Thomas 2011). Since first being proposed by Peters & Darling 1985, assisted colonisation has attracted significant debate over its use as a climate change mitigation technique due to the complex policy, ecological and ethical questions that it raises (Hoegh-Guldberg *et al.* 2008; Ricciardi & Simberloff 2009a, b; Hewitt *et al.* 2011). One of the main concerns is that translocated species will have similar impacts to invasive alien species, including uncontrolled population growth and negative effects on native taxa (Ricciardi & Simberloff 2009a). In addition to the potential risks attached, assisted colonisation attracts debate because it conflicts with established conservation models that favour maintaining the status quo of species ranges and *in situ* management (Hayward 2009). However, as previously highlighted in this review, these established conservation models may not suffice in the fight to prevent the extinction of species and populations that cannot adapt *in situ* to rapid climate change. In recognition of this, there have been a growing number of frameworks that aim to help conservation practitioners in making the decision as to whether a species is a candidate for assisted colonisation (e.g. Hoegh-Guldberg *et al*. 2008; Richardson *et al.* 2009; Pérez *et al.* 2012; Schwartz *et al.* 2012).

Currently, examples of bird assisted colonisation attempts remain scarce within the peer-reviewed literature, with the bulk of published articles documenting the movement of plants (e.g. Liu *et al.* 2012; Isaac-Renton *et al.* 2014; Castellanos-Acuña *et al.* 2015). However, translocation in the form of reintroduction has been used extensively for rare and vulnerable bird species in countries such as New Zealand, with demonstrable success (e.g. Taylor *et al.* 2005; Miskelly & Powlesland 2013). Many of these translocations involved the movement of individuals from one island to another, after the species had undergone considerable declines due to the introduction of invasive mammals (Miskelly & Powlesland 2013). Although the type of threats may be different, parallels can be drawn between the adaptive capacity of island and montane-restricted biota, so much so that mountain environments are often referred to as 'sky islands' for the species that inhabit them (e.g. McCormack *et al.* 2008; Bech *et al.* 2009; Manthey & Moyle 2015). As opposed to being surrounded by inhospitable marine habitat like conventional islands, sky islands are surrounded by inhospitable terrestrial lowland habitat. In both cases, the inhabitants of the islands are unlikely to cross the expansive masses of unsuitable habitat to access suitable environments elsewhere, irrespective of the threats they may face on their islands. For temperate sky island species and populations such as the two subspecies of Rock Ptarmigan (*Lagopus muta pyrenaica* and *L. muta helvetica*) in southern Europe, or the Mountain Pipit *Anthus hoeschi* in the Lesotho highlands, their mountaintop distributions makes them particularly vulnerable to climate change. As climate change advances, their range sizes are projected to contract as their lower altitudinal range boundaries shift further upslope (Revermann *et al.* 2012; BirdLife International & Durham University 2017). If these species and other montane specialists fail to adapt, extinction would be inevitable due to the finite amount of space available in mountain systems for tracking their climatic niche. Therefore, if suitable sites can be identified in mountainous regions where future persistence is predicted to be high, assisted colonisation can offer a lifeline to montane bird populations that may otherwise become extinct. The identification of these areas of long-term persistence is possible with the use of SDMs (Schwartz 2012; Guisan *et al.* 2013), and by integrating intermediate dispersal scenarios into the modelling process, practitioners can filter out those areas within the natural dispersal reach of a species. Nevertheless, it is possible that for some highly specialised species there may not be suitable habitats elsewhere.

Targeted gene flow

An alternative resilience-focused management strategy for minimizing biodiversity loss under climate change is targeted gene flow (TGF), which involves moving individuals within their existing range to introduce specific adaptive traits into a recipient population (Hoffmann & Sgrò 2011; Aitken & Whitlock 2013; Macdonald *et al.* 2017). The complexity of implementing TGF is one of its major shortfalls; however, it potentially carries far fewer ecological risks than assisted colonisation because species are not being introduced to ecosystems outside of their indigenous range. In contrast to traditional management strategies like the creation and management of protected areas, which could essentially contribute towards the conservation of all species, TGF requires certain criteria based on a species' genetic diversity in order to implemented (Sgrò *et al.* 2011). Based on evolutionary and ecological theory, the best place to look for TGF source populations is on the peripheral edges of a species range (Macdonald *et al.* 2017), where sufficient isolation has nurtured the evolution of phenotypically adapted individuals to certain climatic conditions. These peripheral isolate populations can provide evidence of what a species is capable of adapting to and may also provide the genetic material required to increase the adaptive capacity of core populations – the key goal of TGF. The adaptive usefulness of these peripheral isolate populations is supported by recent rediscoveries of presumed-extinct species of mammals (Fisher 2011) and frogs (Puschendorf *et al.* 2011) which were found on the edges of their former ranges.

In the case of temperate montane birds, isolated populations with ranges at lower altitudes and closer to the equator could possess the genetic diversity capable of increasing the adaptive capacity of core populations under the progressing effects of climate change. Despite the fact that peripheral habitats may contain populations that are pre-adapted to the future climatic conditions of core areas, these populations may also be at a greater risk from climate-induced extinction due to their small size, isolation and marginal climate (Gaston & Fuller 2009). A number of montane Galliform species exhibit high levels of genetic differentiation between their isolated populations (e.g. Gutiérrez *et al.* 1983; Segelbacher and Piertney 2007; Klinga *et al.* 2015), as well as being at a high risk from the effects of climate change (e.g. Revermann *et al.* 2012; Henden *et al.* 2017). Similarly, research has shown that a peripheral population of a high-alpine passerine in the Cantabrian Mountains of north-eastern Spain contained a haplotype that was absent in populations from other mountain ranges in Europe (Resano-mayor *et al.* 2017). For these species, provided they have distribution patterns that consist of multiple populations that are spread across the landscape, with isolated populations that have adapted to climatic conditions that will emerge and/or persist under future climate change, TGF is a potentially useful management strategy. However, TGF will not be suitable for species that are restricted to a single mountain range, or have populations with high levels of gene flow, the former of which represents many of those most at immediate risk from climate change (La Sorte & Jetz 2010).

2.6 Weighing up options for montane bird conservation

Climate change is occurring at a time when global biodiversity is already under pressure from a host of anthropogenic threats (e.g. land-use changes, urbanization, hunting and pollution). The focus of this review has primarily been restricted to management strategies aimed at mitigating climate-related threats to montane birds. However, management strategies that integrate and counteract multiple threats and achieve multiple conservation objectives must be prioritised over those that only target a single stressor.

Despite the commonalities in the plight of temperate montane birds, it is unlikely that there will be a ‘one strategy suits all’ approach to their conservation under the changing climate. It is likely however that certain traits may cause a species to be particularly vulnerable to climate change (e.g. Foden *et al.* 2013; Pearson *et al.* 2014; Pacifici *et al.* 2015), and in turn, certain management strategies may be more appropriate for species that possess those traits. In Table 2.1, the management strategies highlighted in this review have been integrated with the three dimensions of climate change vulnerability (exposure, sensitivity and adaptive capacity) identified by Foden *et al.* 2013 in order to propose the most suitable management strategy for species that fall into each dimension, or combination of dimensions. However, those responsible for conserving montane species are likely to find themselves in a situation where they require additional data and research on their species, particularly over larger spatial scales, in order to adequately determine the vulnerability and most appropriate management strategy for their focal species. Therefore, research needs are outlined that would help to fill data and knowledge gaps preventing practitioners from better assessing the most appropriate strategy for their focal montane species. Although these research areas are designed with birds in mind, similar strategies will improve the chances of preserving a vast proportion of montane-restricted biodiversity under climate change.

Table 2.1 Management strategies for montane species under climate change and future research areas for improving vulnerability assessment and management strategy choice. The three climate change vulnerability dimensions identified by Foden *et al.* 2013 have been integrated with three management strategies outlined in this review in order to outline the most suitable management approach for species that exhibit certain combinations of vulnerability.

Management strategy	**Vulnerability dimensions**
Management and creation of Protected Areas *This technique alone is applicable to montane species that are at risk from advancing climate change but are likely to persist in situ.*	*Exposed, but not sensitive*
Areas for future research: • Regular monitoring of avifaunal montane community composition inside protected areas and biodiversity hotspots. Particular focus should be paid to the presence of newly colonising species that could compete with natives through interference or the exploitation of important resources (e.g. nesting sites or food). These novel interspecific interactions should be recorded in order to explore the impacts on indigenous montane specialists (e.g. Harris & Siefferman 2014) and if deleterious, could help inform future management approaches. • Basic biodiversity monitoring and documentation of species' distributions in order to better inform climate change management strategies (Chamberlain *et al.* 2012). This is required even in 'well studied' regions such as Europe (EEA 2010), but particularly in the temperate mountain ranges of central Asia where data deficiency is a real problem for a number of montane species (e.g. Sillem's Rosefinch *Carpodacus sillemi* and Altai Snowcock *Tetraogallus altaicus*). This area of research could technically support the assessment and applicability of every management strategy but it has been included here because often one of the first conservation priorities will be ensuring a species' representation within protected areas. • The availability and use of microrefugia by birds in montane protected areas. This is well documented in plants (e.g. Stewart *et al.* 2010) and if there is similar utilization by birds, it could allow them to persist in equatorial and lower altitude mountain ranges for longer than many broad-scale climate models predict.	
Assisted colonisation *This technique is applicable to montane species that are at risk from advancing climate change, are unlikely to persist in situ and have a limited capacity to adapt through means of dispersal.*	*Exposed, highly sensitive and low adaptive capacity*
Areas for future research: • Further research into the processes that drive both short and long-distance dispersal in birds. Thousands of birds, some of which are montane specialists (e.g. Alpine Accentor *Prunella collaris*), regularly turn up as vagrants hundreds of kilometres from their nearest breeding or wintering areas. If some of these individuals turn up in mountainous localities that possess suitable conditions for breeding, could they then establish viable populations at these localities? (E.g. White-winged Snowfinch *Montifringilla nivalis* recent colonisation of the Corsican Mountains, Thibault & Bonaccorsi, 1999). With improved data collection and an understanding of dispersal, conservation practitioners could determine the necessity of assisted colonisation –species with high levels of dispersal (e.g. Bearded Vulture *Gypaetus barbatus*, Margalida *et al.* 2013) may have the ability to reach climatically suitable mountains without assistance. • Develop a list of species to consider for assisted colonisation based on SDM projections. Once the	

list has been developed, extant populations can be monitored in order to detect when action is likely to be required. If action is required, SDM projections can guide decision makers to sites (if existent) that will persist under future climate change (Schwartz 2012), then site surveys can be carried out in order to determine the suitability of the site for the species in question.
- Identify the functional role that potential assisted colonisation candidate species play in their current ecosystems. Many bird species hold important functions in their ecosystems (e.g. seed dispersal, creation of nesting cavities and pest control) that may be transferable to ecosystems at relocation sites (this additional motivation has been proposed by Lunt *et al.* 2013). With this acquired knowledge, potential losses for the species native ecosystem, and potential gains for the ecosystem at the proposed introduction site can be established.
- Understanding when a given species will become invasive in a given context. The most widely criticised element of assisted colonisation is its potential to introduce taxa that becomes invasive within a recipient ecosystem (Mueller & Hellmann 2008). Efforts to reduce the uncertainty surrounding invasive potential would greatly improve the assisted colonisation decision-making process.

Targeted gene flow *This technique is applicable to montane species that are at risk from advancing climate change but have the spatial distribution pattern to harbour genetically differentiated populations.*	*Exposed, highly sensitive with potential genetic adaptive capacity*

Areas for future research:
- Despite the promising theory behind TGF, the approach remains within its infancy, with a lack of case studies from which conservation practitioners and policy makers can use to inform their own projects (Macdonald *et al.* 2017). However, community groups and government agencies are already performing TGF (e.g. Weeks *et al.* 2015), therefore, research focusing on the improved documentation and information outreach of these processes would be hugely beneficial for other conservation practitioners contemplating TGF.
- Greater co-operation among bird ringing groups and organisations. This could provide vital information on species-specific adaptive capacities through their levels of natal and breeding dispersal (e.g. the dispersal estimates of U.K birds in Paradis *et al.* 1998), which in turn could provide indication of whether there is exchange between certain populations (i.e. the identification of potential isolates). Dispersal data deriving from international ringing schemes would be of most use, for example, the organisation EUring collects data from ringing groups across the European continent, which could provide insightful information on the exchange of species units between populations over the wider landscape.
- The use of genetic tools to assess gene flow across a species distribution. Similar to data on dispersal, this would give further (and more detailed) indication as to which montane populations are isolated and have high levels of genetic differentiation. This could determine the suitability of TGF for the focal species and guide practitioners to the ideal candidate populations (e.g. Resano-mayor *et al.* 2017).

2.7 Conclusion

The future persistence of temperate montane bird species under climate change will be reliant on a mixture of the management strategies outlined in this review. Conservation practitioners should identify how montane species fit into the vulnerability framework presented by Foden *et al.* (2013) before planning and determining the most appropriate management approach for their focal species. The broad and far-reaching impacts of the changing climate will require regionally coordinated management actions that extend beyond the borders of most typical patch-focused conservation projects. Regional coordination should be an integral component of efforts made to fill in the data and knowledge gaps (e.g. dispersal and genetic differentiation) that are required to more rigorously assess the vulnerability and choice of management strategy for many montane species.

Chapter 3

European alpine birds under climate change - can they make it on their own?

Abstract

Climate change has already caused changes to the distributions of many species, leading to severe range contractions and population declines. I aimed to project areas of future suitable climate for European alpine birds under climate change in order to identify and assess potential assisted colonisation (AC) sites for the conservation of these species. I incorporated dispersal estimates into the modelling process in order to establish whether a species could colonise unoccupied climates without human intervention. Climatically suitable areas beyond dispersal reach were filtered in order to identify sites that will sustain their climatic suitability under long-term climate change. These sites were deemed potential AC recipient sites and were assessed in terms of their habitat suitability and protected area coverage for each species. The climatic conditions at these sites were then compared to the conditions currently inhabited by existing populations using a principal components analysis in order to determine which populations may be best adapted to potential AC sites. I predict that European alpine birds will lose a considerable proportion of their climatically suitable space under future climate change (57-80% by 2080 under limited dispersal), with particular losses projected to occur in Europe's southerly distributed mountain ranges (e.g. Balkan and Iberian Peninsulas). I identified potential AC sites for the majority of alpine species - the most commonly projected site was located in the Western Carpathians, with the amount of suitable habitat ranging from 154 to 269 km^2 depending on the species' habitat requirements. The findings presented here are useful for guiding conservation practitioners to the most suitable AC sites for alpine birds under climate change, and the most suitable source populations for translocating to those sites.

3.1 Introduction

Climate change is recognised as posing a significant threat to biodiversity worldwide (Thomas *et al.* 2004; Cahill *et al.* 2012). The average global surface temperature increased by 0.85°C during the period between 1880 and 2012, and this warming trend is forecast to accelerate in the future (IPCC 2014). Species are responding to climate change in a variety of ways, such as altering their phenological events (Walther *et al.* 2002), changing their biotic interactions (Tylianakis *et al.* 2008) and shifting their distributions (Chen *et al.* 2011). Distribution shifts are generally poleward and upward in elevation (Hitch & Leberg 2007; Tingley *et al.* 2012; Gillings *et al.* 2015), leading to range expansions for some species (e.g. Davey *et al.* 2012; Massimino *et al.* 2015) and retractions for others (e.g. Beever *et al.* 2011; Giersch *et al.* 2014). Predicting the impacts of these climate-induced changes has become an extremely active research field (Bellard *et al*. 2012), as these predictions can identify future risks to biodiversity and inform conservation planning and decision making (Guisan *et al.* 2013).

Mountain regions are particularly threatened by climate change (Beniston 2003; Williams *et al.* 2007; Brunetti et al. 2009) and exhibit a higher rate of warming compared to the global average (Böhm et al. 2001). The highest temperature increases are projected to occur in mountains of the northern latitudes (Nogués-Bravo *et al.* 2007). These warming temperatures are predicted to have serious implications for biodiversity (Şekercioğlu *et al*. 2008), and are particularly worrying for range-restricted and endemic species, a high proportion of which are restricted to mountains (Essl *et al*. 2009). Elevational shifts of mountain-dwelling bird species in response to these warming temperatures have been documented around the globe (e.g. Tingley *et al.* 2009; Maggini *et al.* 2011; Freeman & Freeman 2014; Lehikoinen *et al.* 2014). Upslope shifts are likely to leave species with less habitable area as they approach mountain peaks (but see Elsen & Tingley 2015). In extreme circumstances, the climatic niche of some populations may move beyond the mountain peaks, forcing them to disperse elsewhere or become extinct (Şekercioğlu *et al*. 2008).

For species and populations with a high risk of extinction and an inability to adapt through means of dispersal, assisted colonisation may be considered as a management strategy. Assisted colonisation (AC), also termed 'assisted migration' or 'managed relocation' (Hällfors *et al.* 2014), involves physically moving individuals beyond their current range to sites where they can persist in the future. The concept is contentious, and has generated intense debate over the relative benefits and risks associated with the movement of taxa beyond their historical range (Hoegh-Guldberg *et al*. 2008; Ricciardi & Simberloff 2009a, b; Hewitt *et al.* 2011). On the one hand, AC can offer a lifeline to a species or population at risk of extinction, but on the other, the introduced individuals could cause unanticipated ecological or economic damage (Mueller & Hellmann 2008). Some of the contention arguably arises from AC's confliction with established conservation models that favour maintaining the status quo of species distributions through *in situ* management (Hayward 2009). However, the dynamic nature of climate change means that traditional conservation strategies (e.g. protected areas) will not solely suffice in our attempt to halt biodiversity loss.

Species distribution models (SDMs) can be used to aid the decision-making process of assisted colonisation (Guisan *et al.* 2013). SDMs correlate the geographical occurrence data of a species with the geographically corresponding environmental data. In the case of climate change, the assumption is that if models can predict current species distributions using recent climatic data, they will also be able to reliably project future changes in distribution using projected future climate data (Huntley *et al*. 2006). The outputs from these models can establish whether a species or population is at risk of decline or extinction under climate change (Hoegh-Guldberg *et al.* 2008; Thomas 2011). If this is the case, SDMs can aid the identification of potential assisted colonisation recipient sites, which may be climate refugia within the current range, or newly emerging sites beyond the species’ current range (Schwartz 2012; Guisan *et al.* 2013).

As a result of the difficulties associated with biodiversity monitoring and research in mountainous environments, studies on alpine birds have been relatively scarce compared to those focusing on lowland species in farmland and forest habitats (EEA 2010; Chamberlain *et al.* 2012). Mountain-restricted species are regularly cited as ideal candidates for AC (Hoegh-guldberg *et al.* 2008; Loss *et al.* 2011; Thomas 2011), as they occupy climatic conditions that are particularly threatened by climate change and have a finite amount of space for which they can track their climatic niche. However, their candidacy remains untested, and with recent research documenting climate-induced declines for montane birds in Europe (e.g. Lehikoinen *et al.* 2014; Flousek *et al.* 2015), there is a need for alternative management strategies such as assisted colonisation to be assessed. Here, I apply SDMs to predict the future distributions of European alpine bird species under climate change and identify and assess potential assisted colonisation sites for these species. I incorporate species dispersal limitations into the modelling process in order to establish whether a species could colonise unoccupied climates without human intervention. Climatically suitable areas beyond probable dispersal distances of the species are deemed potential AC recipient sites and are assessed in terms of their habitat suitability and protected area coverage. I use a novel approach to identifying source populations for AC sites, by comparing the climatic conditions between source populations and those at potential AC sites through a principal components analysis niche comparison technique. I infer that populations with higher climatic niche overlap would be more suitable as potential AC candidates.

There is a call for scientific researchers to make more of an effort to consider conservation decision making in their work (Cayuela *et al.* 2009; Guisan *et al.* 2013). With this in mind, the results are specifically focused on potential conservation actions, in the form of assisted colonisation, which could be undertaken in the near future (up to 2050) and remain effective over a longer time frame (up to 2080). Less emphasis is put on areas that do not sustain climatic suitability in the long-term (though these areas are acknowledged) or areas that only become suitable towards the end of the century. I also acknowledge the potential caveats of the approach taken and recommend a number of actions that should be considered before any decisions are made.

3.2 Methods

Species data

The focus of this research was on alpine bird species with breeding distributions that are restricted to mountainous environments chiefly on or above the treeline in Europe (Citril Finch breeds on the fringes of the Alpine zone, utilizing semi-open coniferous forest for nesting and alpine meadows for foraging (Cramp & Perrins 1994; Förschler 2001; Borras *et al.* 2003)). This criterion resulted in a total of seven species (see Table 3.1 for an ecological summary of each species). This included one exception to the aforementioned criterion, the Rufous-tailed Rock-thrush, which may tolerate rocky habitats at altitudes as low as 500m in Europe, but has declined substantially in these lower alpine areas and is now more restricted to open habitats above the treeline (Snow *et al.* 1997; BirdLife International 2017). I downloaded occurrence data for these seven species from the Global Biodiversity Information Facility (GBIF) and eBird. The occurrence data underwent a filtering process to remove duplicate records. eBird share their data with GBIF on an annual basis so I only incorporated eBird records uploaded between 01/01/16 and 17/01/17 to further avoid duplication. I also removed historical records (pre-1950). I removed records considered erroneous based on the known breeding distributions of each species i.e. records falling outside the distributions recognised by a range of sources (e.g. See Appendix 1). I opted for this multi-source approach during the occurrence data refinement process as I found that certain populations had been overlooked by certain sources. Species-specific records that occurred within the known European breeding range of each species were retained, while those that occurred outside the known range were removed.

Table 3.1. Ecological characteristics and current knowledge of the climate-related threats for the seven focal European alpine bird species in the present study. Ecological information and threats for each species are sourced from their individual European Red List profile (see BirdLife International 2015).

Species	**Red List status' European / EU27 status**	**Estimated breeding altitudinal distribution**	**Breeding habitat preference** (level 1 – level 2)	**Migratory status**	**Climate-related threats recognised by BirdLife International**
Alpine Accentor *Prunella collaris*	LC/LC	1800-3000m	-Grassland - Temperate -Rocky areas (e.g. inland cliffs, mountain peaks)	Short-distance migrant	Temperature extremes
Bearded Vulture *Gypaetus barbatus*	VU/VU	1000-4800m	-Artificial/Terrestrial - Urban Areas -Grassland - Temperate -Rocky areas (e.g. Inland cliffs, mountain peaks) -Shrubland - Mediterranean-type Shrubby Vegetation	Resident	Habitat shifting & alteration
Citril Finch *Carduelis citrinella*	LC/LC	1500-2500m	-Forest - Temperate -Grassland - Temperate -Shrubland - Temperate	Short-distance altitudinal migrant	Habitat shifting & alteration
Rufous-tailed Rock Thrush *Monticola saxatilis*	LC/LC	500-3800m	-Grassland - Temperate -Rocky areas (e.g. Inland cliffs, mountain peaks) -Shrubland - Temperate	Long-distance migrant	*Climate-related threats omitted in species profile*
Water Pipit *Anthus spinoletta*	LC/LC	1400-2600m	-Grassland - Temperate -Rocky areas (e.g. inland cliffs, mountain peaks)	Short-distance migrant	Habitat shifting & alteration
White-winged Snowfinch *Montifringilla nivalis*	LC/LC	1000-3160m	-Grassland - Temperate -Rocky areas (e.g. inland cliffs, mountain peaks)	Resident	Habitat shifting & alteration
Yellow-billed Chough *Pyrrhocorax graculus*	LC/LC	1260-3400m	-Artificial/Terrestrial - Pastureland & Urban areas -Grassland - Temperate -Rocky areas (e.g. inland cliffs, mountain peaks)	Resident	*Climate-related threats omitted in species profile*

LC = A taxon is considered 'Least Concern' (LC) when it has been evaluated against IUCN vulnerability criteria and does not qualify for Critically Endangered, Endangered, Vulnerable or Near Threatened.
VU = A taxon is considered 'Vulnerable' (VU) when it has been evaluated against IUCN vulnerability criteria and the best available evidence indicates that it is facing a high risk of extinction in the wild.
Level 1 habitat = General habitat type (IUCN Habitat Classification Scheme Version 3.1; IUCN 2012).
Level 2 habitat = Sub-category of level 1 habitat type, providing more detail on species preference (IUCN Habitat Classification Scheme Version 3.1; IUCN 2012).

Species distribution modelling

Species distribution modelling was carried out within the BIOMOD2 package (Thuiller *et al.* 2013) using R software version 3.1.1. To account for the uncertainty associated with single modelling techniques (Buisson *et al.* 2010), I used the ensemble forecasting function in BIODMOD2 to gain a consensus between three modelling techniques. These included one regression method (Generalized Additive Model) and two machine learning methods (Random Forests and Generalized Boosting Model). In order to evaluate the predictive performance of the distribution models, a random subset of 70% of the data was used to calibrate the models while the remaining 30% was used for evaluation. I used a cross-validation procedure that incorporated the 'area under the ROC curve (AUC)' (Hanley & McNeil 1982), the 'true skill statistic (TSS)' (Allouche *et al*. 2006) and 'Cohen's Kappa Statistic' (Monserud & Leemans 1992). Probabilities of occurrence were transformed into binary maps using the value that maximized the Kappa score as a threshold. The median probability over the selected models was chosen as the median is less sensitive to outliers than the mean (Thuiller *et al.* 2013).

Environmental data

I used six climate variables from the WorldClim database in order to predict current and future species distributions. These included three temperature variables (Max Temperature of Warmest Month (BIO5), Temperature Annual Range (BIO7) and Mean Temperature of Coldest Quarter (BIO11)), two precipitation variables (Precipitation of Wettest Quarter (BIO16) and Precipitation of Driest Quarter (BIO17)) and the annual mean of Potential Evapotranspiration (PET). Temperature and precipitation are expected to impose direct and indirect constraints on bird distributions (Root, 1988; Araújo *et al.* 2009).

I projected 'current' distributions for each species using climate data from the 1961-1990 period at a 10km resolution. Future distributions for 2021-2050 and 2051-2080 were projected using a set of regional circulation models (RCMs) originating from the Eco-change project. This project involved physically downscaling the coarse resolution climate model output of general circulation models (GCMs) to a much finer spatial resolution on a physical process basis. Statistically downscaling high-resolution climate data can show substantial spatial heterogeneity in all climate variables, particularly in mountainous regions (Tabor & Williams 2010). Therefore, these high resolution climate datasets can allow for more spatially detailed projections of future species distributions and extinction risks in alpine environments. I used three different RCMS, the HadRM3, RACMO2 and RCA30 (Collins *et al.* 2006; Jones *et al.* 2004a; Jones *et al.* 2004b; Van Meijgaard *et al.* 2008), that were fed by three different GCMs (HadCM3, ECHAM5 and CCSM3; see

Mitchell *et al.* 2004) and this resulted in four RCM/GCM combinations. I used the results of the A1b emission scenario (Nakicenovic *et al.* 2000), which represents a medium-to-high level of warming (1.7–4.4 °C) for presenting results, though projections under the B1 (Lower; 1.1 - 2.9 °C) and A2 (high; 2–5·4 °C) emission scenarios were also made (see Table 3.2 for a list of the climate model scenarios made available by the Ecochange project). The extent of the downscaled climate projections was: Longitude: West: 10.535, East: 31.775, Latitude: North: 65.670, South: 34.833, therefore, this was the extent of the study area considered within the study.

Table 3.2. Climate model scenarios run to assess the impact of climate change on European alpine bird species. Regional Circulation Models (RCM) are labelled in bold, while the General Circulation Models (GCM) used to feed the RCMs are in normal font. The three emissions scenarios (A1b, A2 and B1) were taken from the IPCC's Special Report on Emissions Scenarios (SRES). Each climate scenario was made available by the Ecochange project.

Model RCM/GCM Scenario:	**A1b**	**A2**	**B1**
RCA30/CCSM3	x	-	-
RACMO2/ECHAM5	x	-	-
HADRM3Q0/HADCM3	x	-	-
RCA30/ECHAM5	x	x	x

Accounting for dispersal

In order to simulate species-specific dispersal constraints, I used a cellular automaton model as implemented in the 'MigClim' package in R (Engler *et al.* 2012). Due to the low levels of occurrence data in parts of Europe, I used the binary projected 'current' distribution output maps from the aforementioned SDMs at a 10km resolution in order to account for the areas of poor data coverage (see Figure 3.1 for maps). I refined these presence/absence maps by removing grid cells that fell outside the species' known extent of occurrence in Europe (following the same method outlined in the Species Data section, see Appendix 1 for sources), thus allowing the dispersal simulations to begin from a more realistic starting point. I changed predicted presence cells to absent during the refinement process; at no point were predicted absence cells changed to present. I chose to manually refine the SDM outputs as opposed to using extent-of-occurrence polygons from published literature, as these tend to over-estimate a species' actual distribution (Graham & Hijmans 2006; McPherson & Jetz 2007b). In the case of European alpine species, this generalisation of species ranges can be especially exaggerated in larger mountain ranges such as the Alps and Pyrenees, where a single continuous polygon is often drawn around the entire mountain range to represent species presence. This type of approach makes the assumption that every 10 x 10 km cell within the polygon boundaries contains suitable climatic conditions for the species in question, when in reality this is unlikely to be the case.

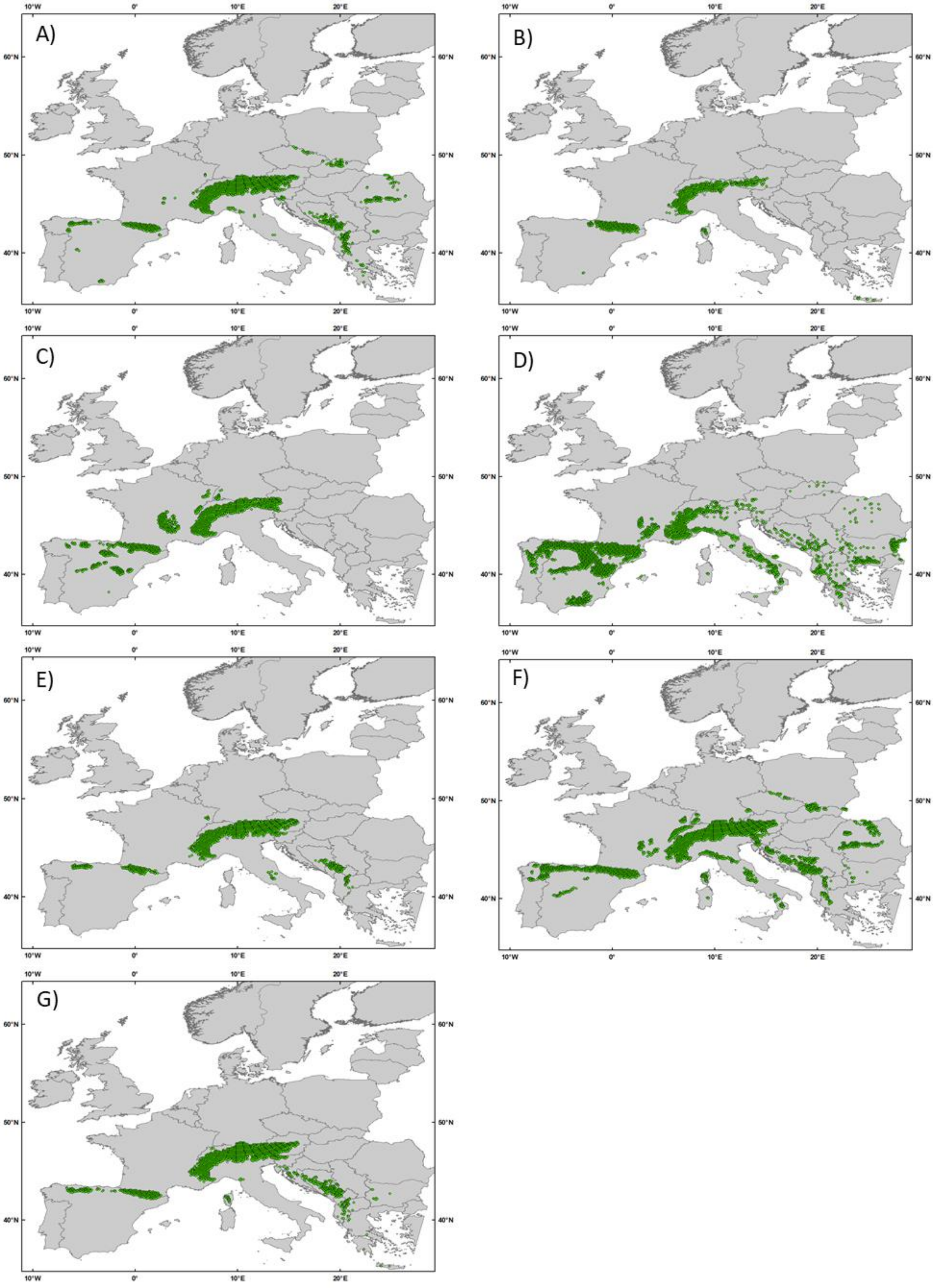

Figure 3.1 Current distributions for seven European alpine bird species. Maps represent projected current distributions that have been refined based on each species' known occurrence in Europe (see Appendix 1 for sources). A) Alpine Accentor *Prunella collaris*, B) Bearded Vulture *Gypaetus barbatus*, C) Citril Finch *Carduelis citrinella*, D) Rufous-tailed Rock Thrush *Monticola saxatilis*, E) Water Pipit *Anthus spinoletta*, F) White-winged Snowfinch *Montifringilla nivalis*, G) Yellow-billed Chough *Pyrrhocorax graculus.*

MigClim was initialized to model the dispersal of each species over a period of 70 years from current to 2050 and 2051 to 2080, reflecting the period covered by the climate change projections. In total, there were 70 dispersal steps in each species' model, representing one dispersal step per year. I calibrated the MigClim dispersal model separately for each species, sourcing values for its key parameters from the relevant literature (see Appendix 2 document for a list of sources and values). When considering the dispersal distance parameter (dispKernel), I followed the approach taken by Barbet-Massin *et al.* 2012, in which the mean (+SD) natal dispersal estimates of closely related species with sufficient capture re-capture data are used as a proxy. This data derives from a long-term ringing scheme analysed by Paradis *et al.* 1998. I made efforts to obtain species-specific dispersal estimates for each of the focal species through contact with various experts and data-holders but I was unable to obtain these due to an insufficient number of ring recoveries required to make an accurate estimate. Long-term dispersal data with sufficient recoveries from a range of locations is often more difficult to obtain for alpine species due to the challenges associated with biodiversity monitoring in remote and mountainous environments.

Grouping populations

In order to quantify potential regional population losses and measure levels of climatic niche overlap, populations of each alpine species were grouped based on the mountain ranges they inhabit. I used the mountain boundaries identified by the Global Mountain Biodiversity Assessment (GMBA) (Körner *et al.* 2017, Figure 3.2) to group populations depending on their location (for mountain definition see Körner *et al.* 2011). In most cases, the species distributions fell within the mountain boundary polygons identified by the GMBA. However, there were a small number of sites currently supporting populations of species in this study that were not recognised as mountains by the GMBA, as they did not meet the definition's ruggedness requirement (see Körner *et al.* 2017). These include the Bohemian Forest, Monte Faro, Monte Gargano, Southeast Iberian Range and the Sudetes Mountains.

In some of the more expansive mountain ranges with substantial areas of forest habitat (e.g. Carpathian Mountains), populations of alpine species appeared less aggregated due to the fragmented orientation of the suitable habitat. I split these populations if two criteria were met. Firstly, the edges of the nearest two 10 x 10km cells were beyond the species' Euclidean mean (+SD) natal dispersal distance of each other and secondly, if the extent-of-occurrence polygons (BirdLife International 2016) for the populations in the area of interest were separated from one and other. The positioning of the population with respect to other populations in the mountain range determined whether I described it as 'upper' or 'lower'. I considered distributions that span across multiple mountain boundary lines to represent one continuous population. Similarly, in order to be considered as one population, the edges of the cells were required to be within the species' mean (+SD) Euclidean natal dispersal distance of each other. For example, the Pyrenees, Montes Vascos and the Cantabrians form a mountainous belt across northern Iberia and a number of species, such as the Water Pipit, breed throughout this belt (BirdLife International 2017). Under these circumstances, individual mountain ranges would be considered as harbouring a single population.

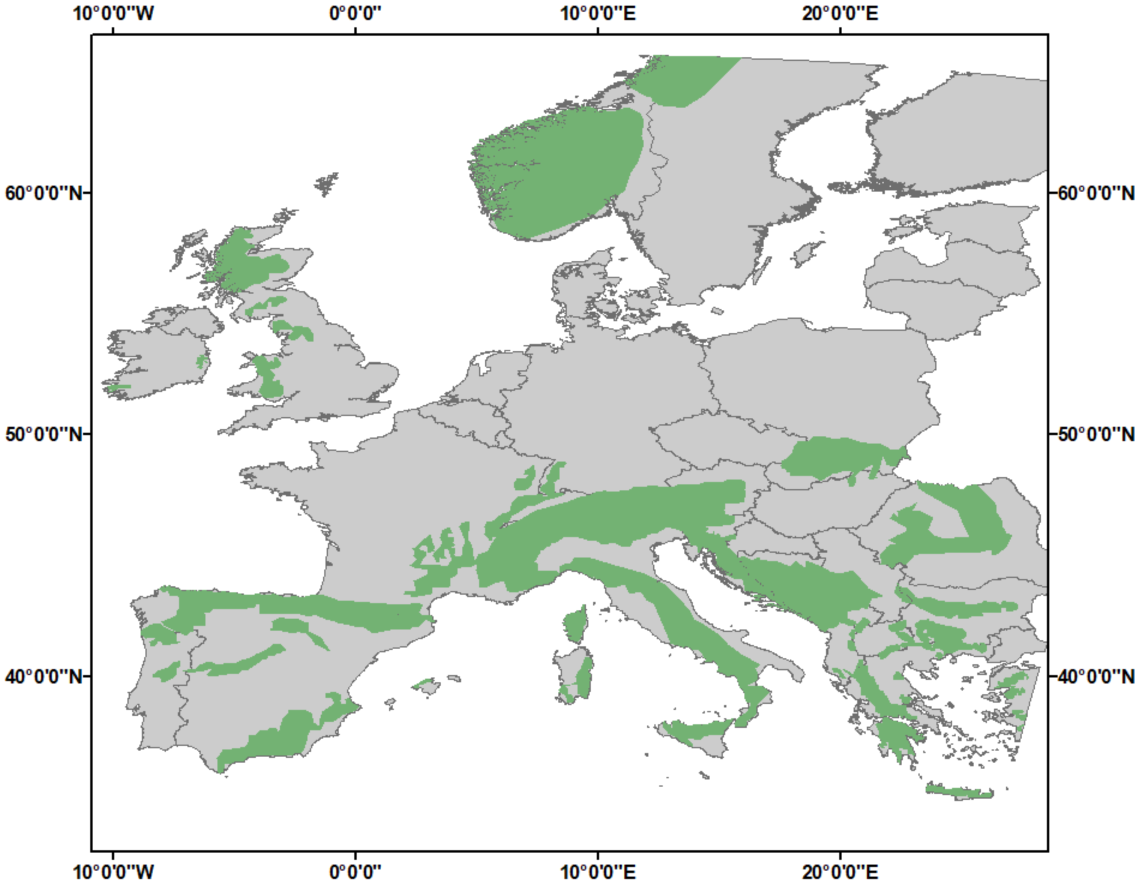

Figure 3.2 European mountainous regions, as defined by the Global Mountain Biodiversity Assessment (GMBA) (see Körner *et al.* 2011; 2017 for mountain criteria). Areas in green represent mountains defined by the GMBA.

Identifying sites for assisted colonisation

Potential assisted colonisation (AC) sites were identified as groups of climatically suitable cells (>3 10 x 10km cells) not currently inhabited by a species and that remained uncolonised during the dispersal simulations (see Figure 3.3 for visualisation of process of identifying (and assessing) potential AC sites). In order to distinguish between potential AC sites, I considered groups of cells as forming a single AC site if the cells were within the mean (+SD) Euclidean distance of the species' natal dispersal estimate of each other. However, there were two potential AC sites in the Western and Eastern Carpathians which I chose to split in two (Upper and Lower). Both habitat composition and protected area coverage varied quite drastically between the northern and southern sections of these two sites. With one of the key aims of assisted colonisation being to enhance the survival prospects for the species being moved (Pérez *et al.* 2012; Gallagher *et al.* 2014), I felt that this was valuable information to the conservation practitioner and could aid the decision-making process in choosing the highest quality release site (see Hodgson *et al.* 2009).

In order to avoid confusion when presenting the results, I refer to the 2021-2050 and 2051-2080 distribution projections as 'near future' and 'distant future' respectively. I only considered cells that became suitable during the current and/or near future projections and remained suitable until the end of the modelling period (distant future) for conducting a more detailed species-specific suitability assessment (i.e. assessing habitat suitability and protected area coverage). The importance of identifying sites that will sustain their suitability under the changing climate is outlined by the IUCN (2013).

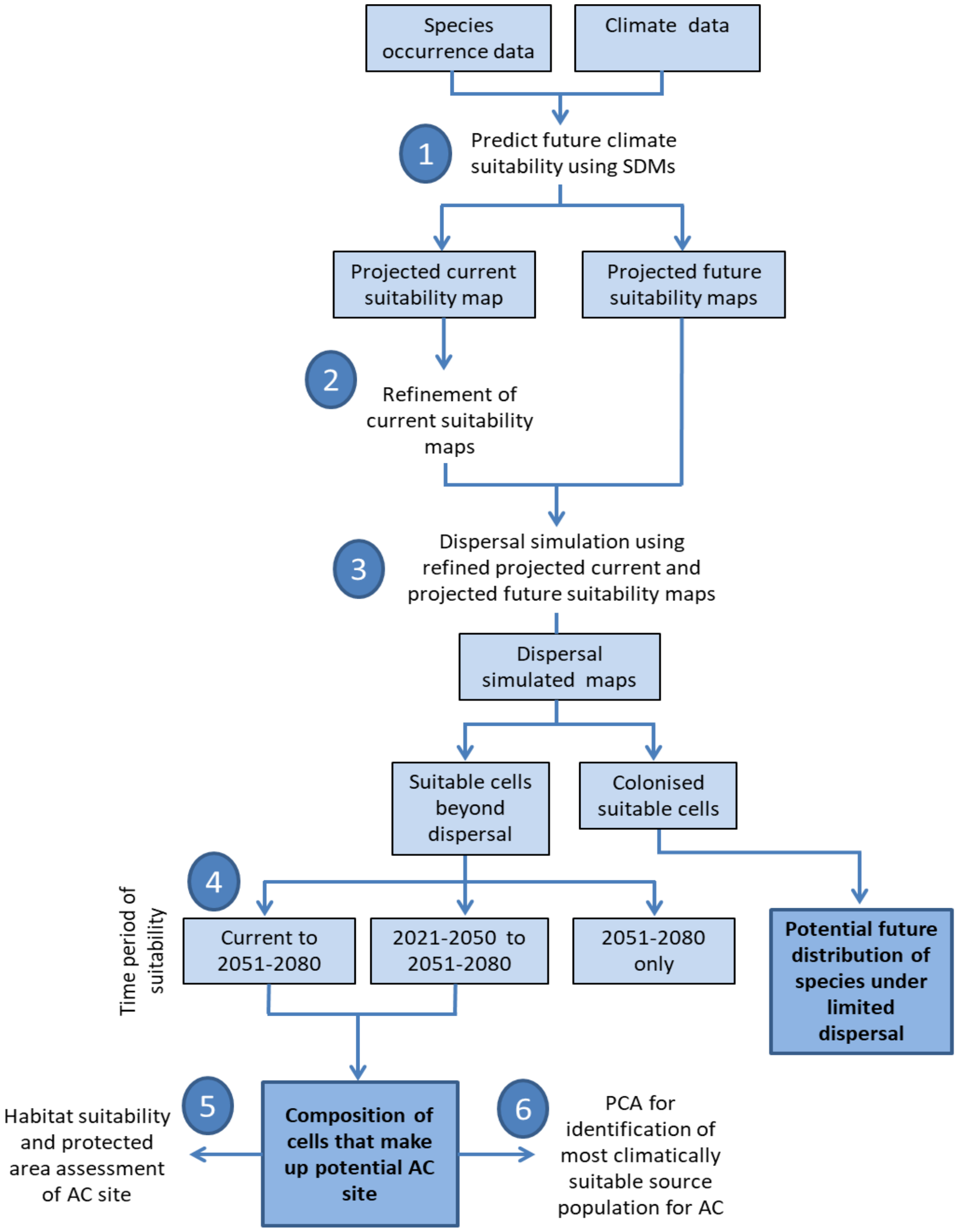

Figure 3.3 Method for identifying and assessing potential assisted colonisation (AC) sites for European alpine birds under climate change. **1)** Occurrence data from GBIF and eBird was used to predict the future climatic suitability for alpine birds at a 10km resolution using Species Distribution Models (SDMs). **2)** Current suitability maps were refined based on published estimates of species' distributions to create more accurate starting points for dispersal simulations (occurrence data was incomplete in certain parts of the study area, thus, refined suitability maps provided a more realistic depiction of species' ranges). **3)** Dispersal simulations were run using the MigClim package in R; species mean (+SD) natal dispersal estimates were used to determine climatically suitable cells that could be colonised by a species. **4)** Climatically suitable cells that were beyond reach of a species (i.e. remained uncolonised) during the dispersal simulations and were projected to become suitable in the current or 2021-2050 time periods and remain suitable until 2051-2080 were considered as potential AC sites providing they were >3 10 x 10km cells in size and within the mean (+SD) Euclidean distance of the species' natal dispersal estimate of each other. **5)** Potential AC sites were assessed in terms of their breeding habitat suitability and their protected area coverage (Natura 2000 network/Nationally designated areas). **6)** Principal components analysis (PCA) following the PCA-env method outlined by Broennimann *et al.* (2012) to identify the most suitable source populations for potential AC sites. By comparing the climatic conditions between the ranges of existing populations and those of potential AC sites, the population that may be the best adapted to site conditions is determined.

Habitat suitability

Habitat preferences were taken from each species' European Red List profile (BirdLife International 2017). BirdLife International has adopted the IUCN habitat classification criteria (IUCN 2012) and assigns suitability ratings to habitat types for every bird species. I harmonized this classification scheme with that of the CORINE Land Cover (2012) inventory in order to assess breeding habitat suitability at each potential AC site (Appendix 3 Table A3.1). I downloaded the CORINE Land Cover raster at a 250m resolution and clipped it for each potential AC site. Areas of 'Suitable' habitat were deemed as those that were specified by Birdlife International as being suitable for the breeding of a species (see Appendix 3 Table A3.1 for a list of habitat suitability classifications for each species). For each potential AC site identified as having suitable climate for a species, the proportion and total area (km^2) of suitable habitat was calculated. Under the IUCN habitat classification criteria (2012), some habitats are classed as of 'major importance' for breeding, meaning they are either an absolute requirement for the species at some point in its breeding life cycle, or the primary habitat type used by most of the individuals from the species (IUCN 2012). In order to avoid potential AC sites appearing to have high habitat suitability despite not having habitats of major importance present, I ensured that at least 5% of the suitable habitat was made up of each habitat of major importance. If this arbitrary threshold was not met, then the habitat suitability assessment was not presented for the site as the species would be unlikely to persist there without habitats that it is reliant upon. All analyses were undertaken in ArcGIS 10.2.2.

The one exception to this thresholding rule was when 'Rocky areas' were classed as of major importance for a species. These 'Rocky areas' include boulders, caves and cliffs, and are the preferred nesting habitat for most species in this study (BirdLife International 2017). Only a small patch of this habitat is required to support a nest (the largest being 1m x 1m for a Bearded Vulture nest) and it is abundant throughout European mountain landscapes. However, it is often distributed amongst other more dominant land-use types and would therefore be unlikely to constitute the predominant land-use type in a 250 x 250m CORINE plot. Therefore, I did not apply a threshold requirement for this habitat classification.

The assessment of habitat suitability made here only takes into account present land cover. It does not take in to account future changes in land-cover - particularly changes to the treeline. As a general trend, treelines are expected to increase in both latitude and altitude on a global scale in response to climate change (Kupfer & Cairns 1996; Holtmeier & Broll 2005), though the extent to which this occurs is expected to vary drastically from region to region (Harsch *et al.* 2009). This is particularly relevant for the focal species of this study as six of them are adapted to breeding habitats found above the treeline. Therefore, increases in treeline would reduce the amount of suitable breeding habitat available to them. However, predicting the future treeline is problematic and often incalculable due to a host of potentially influential factors (Holtmeier & Broll 2007), as demonstrated in the Carpathian Mountains (Weisberg & Becker 2013). It is for this reason that the potential treeline changes were not incorporated into the habitat suitability analysis.

Protected area coverage

Protected area coverage for each potential AC site was calculated by overlaying the Natura 2000 network layer with the gridded 250m x 250m CORINE habitat classification layer in ArcGIS 10.2.2. I used the habitat suitability classifications outlined previously to split the habitats at each potential AC site into 'suitable' and 'marginal' for each species. I then calculated the proportion of suitable habitat protected under the Natura 2000 network at each site. For some species, potential AC sites were identified in countries outside of the Natura 2000 network (e.g. Scandinavian Mountains, Norway). I used the European Environment Agency's National designated areas dataset (EEA 2016) to calculate protected area coverage values for these sites. All Natura 2000 and EEA layers were converted to Lambert Azimuthal Equal Area 10/52 projection to match the SDM and habitat layers.

Climatic niche overlap

The most suitable population for each potential assisted colonisation (AC) site was identified using the "PCA-env" ordination technique outlined in Broennimann *et al.* (2012). I opted for this technique over other PCA methods because it summarises the entire range of climatic variability found in the whole study area (i.e. Europe), and it is in this multivariate space that occurrences of the species' populations are then projected. By comparing the climatic conditions between the ranges of existing populations and those of potential AC sites identified by the dispersal-refined SDM outputs, I determined which population may be better adapted to conditions at a potential AC site.

The PCA-env technique incorporates background environments, which I constrained to ecologically plausible regions of occurrence for each species (Barve *et al.* 2011; Tingley *et al.* 2016). This was achieved by clipping the European climate data layer (10 x 10km resolution) with the GMBA polygon layer in ArcGIS 10.2.2. The resulting layer was then refined for each individual species, by removing the climate variable data from mountain ranges where the species does not breed. The exception was for mountain ranges that contained potential AC sites identified by the SDMs. For each PCA-env run, I created a separate set of background environments that only incorporated the climate variable values from the mountain range where the AC site was located. For the five breeding sites that did not meet the GMBA's ruggedness criteria, I only incorporated the 10 x 10km occurrence and AC site cells. Populations or potential AC sites with less than five 10 x 10km cells did not meet the minimum number of values required to run the PCA-env and were therefore not included.

Climate variable values from across the aforementioned background environments in Europe were combined and projected onto the first two axes of a principal components analysis (PCA) for each species. These two PCA axes described the environmental space available to a species and explained the variation in the raw climatic data. This environmental space was then projected onto a grid consisting of 100 x 100 cells, with minimum and maximum values defined by those present in the available background data. A smoothed density of occurrence for each species in each cell of the PCA grid was then estimated using a kernel density function (Broennimann *et al.* 2012). I calculated climatic niche overlap between a population and potential AC site using Schoener's *D*, a metric which expresses an overall fit between niches over the full environmental space. The *D* metric varies from 0 (no overlap) to 1 (complete overlap). I used the *D* metric estimates to test for niche similarity and niche equivalency (Warren *et al.* 2008), following randomization tests as outlined in Broennimann *et al.* 2012. Under the similarity test, a value of <0.05 indicates that niches are statistically more similar than expected at random, while a value of <0.05 in the equivalency tests reveals that niches are not statistically equivalent.

3.3 Results

Model evaluation

The predictive accuracy of the species distribution models was very good for the seven alpine species, with all AUC values above 0.98, TSS above 0.88 and Kappa values above 0.75 (Table 3.3). Accuracy tended to be higher for the more range restricted species (e.g. Bearded Vulture) than those that are more widespread in Europe (e.g. Water Pipit).

Table 3.3 Species distribution model evaluation metrics for the seven focal European alpine bird species.

Species	AUC	TSS	Kappa
Alpine Accentor	0.984	0.887	0.759
Bearded Vulture	0.997	0.955	0.890
Citril Finch	0.990	0.915	0.797
Rufous-tailed Rockthrush	0.995	0.959	0.854
Water Pipit	0.986	0.886	0.787
White-winged Snowfinch	0.992	0.928	0.821
Yellow-billed Chough	0.995	0.932	0.872

Accounting for dispersal

Accounting for dispersal affected the projected future distributions of species in different ways. The greatest proportional changes were evident in the species with the largest distributions in Europe, the Rufous-tailed Rockthrush and the Water Pipit, the former of which varied by more than 50% between the two dispersal scenarios (Table 3.4; Figure 3.4; Appendix 5). The predicted distribution of the Yellow-billed Chough varied the least between the two scenarios, with less than a 5% decrease under the limited dispersal scenario. On average, accounting for dispersal reduced the predicted future distribution sizes by 19.6% (± 6.4%) for the distant future (2080).

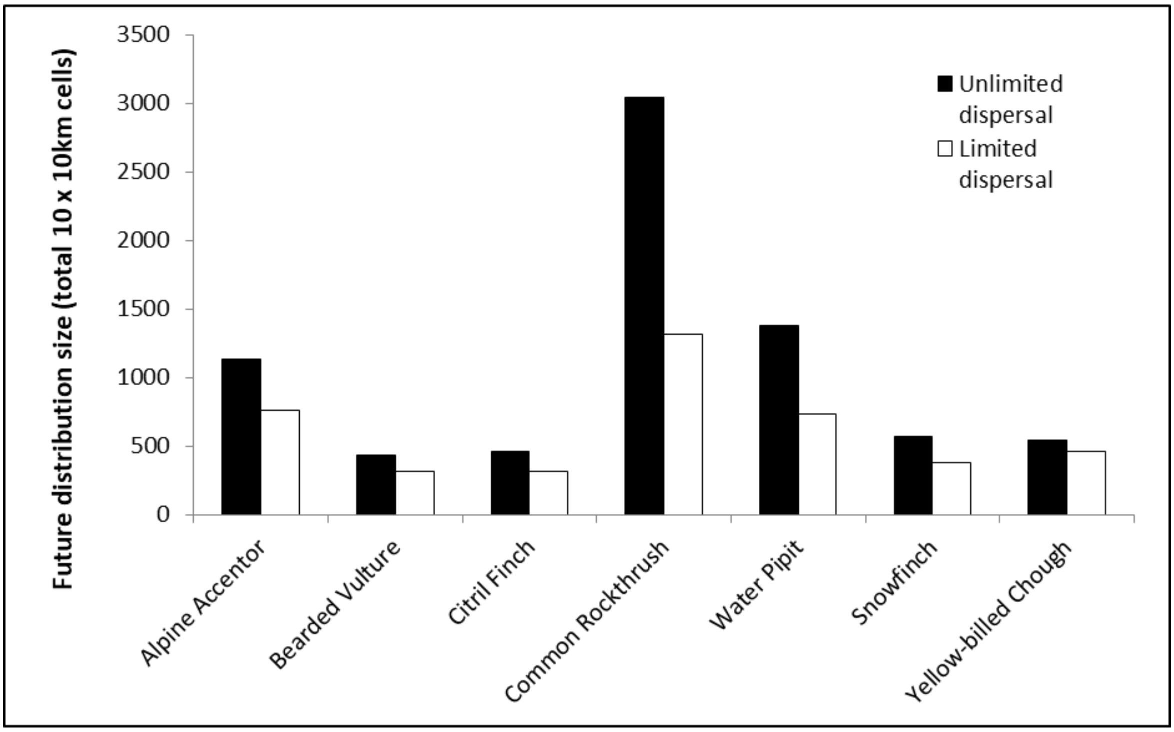

Figure 3.4 Projected distant future (2051-2080) European distribution sizes under two dispersal scenarios under the RCA30 regional circulation model driven by the ECHAM5 general circulation model and based on the A1b emission scenario. The 'unlimited' dispersal scenario assumes that every 10 x 10km cell projected to be climatically suitable for a species can be colonised by a species irrespective of dispersal. The 'limited' dispersal scenario takes in to account a species' mean (+SD) natal dispersal distance and only allows the colonisation of cells within that distance. See Appendix 5 for maps of projected suitable climates and 10 x 10km cells colonised under limited and unlimited dispersal scenarios for 2051-2080. See Appendix 5 for maps of projected distribution under limited and unlimited scenarios.

Table 3.4 Proportional change in areas of suitable climate from current conditions to distant future (2051-2080) for the seven focal European alpine birds. Projections are based on the RCA30 regional circulation model driven by the ECHAM5 general circulation model under the A1b emission scenario and include varying levels of dispersal. The 'unlimited' dispersal scenario assumes that every 10 x 10km cell projected to be climatically suitable for a species can be colonised by a species irrespective of dispersal. The 'limited' dispersal scenario takes in to account a species' mean (+SD) natal dispersal distance and only allows the colonisation of cells within that distance

Species	% loss in distant future under unlimited dispersal scenario	% loss in distant future under limited dispersal scenario
Alpine Accentor	-39.5%	-59.5%
Bearded Vulture	-52.6%	-66.1%
Citril Finch	-70.9%	-79.9%
Rufous-tailed Rockthrush	-2.15%	-57.7%
Water Pipit	-53.3%	-75.1%
White-winged Snowfinch	-61.1%	-73.8%
Yellow-billed Chough	-69.5%	-74.1%

Predicted change in climatic suitability

By the end of the time period considered (2080), the seven alpine species are predicted to lose 57-80% of their current climatically suitable area in Europe under the limited dispersal scenario (Table 3.4). For all species, except the Rufous-tailed Rockthrush, the majority of mountainous regions currently inhabited are projected to become entirely unsuitable within the time frame considered in this study (Appendix 4). Loss of suitability will be most pronounced in the more southerly mountain ranges concentrated in the Mediterranean region (e.g. Iberian and Balkan Peninsulas). In contrast, the Alps are projected to sustain climatic suitability for every species throughout the time period considered, although are still forecast to decline in overall suitability. The Pyrenees are similar, though not for all species and projections indicate that the region will become entirely unsuitable for the Bearded Vulture by the distant-future. In the near-future time-period, some of the more northerly mountainous regions such as the Jura Mountains and Vosges are projected to temporarily increase in suitability for a number of species (e.g. Alpine Accentor, Citril Finch, Water Pipit), before decreasing in suitability again by the distant-future.

Identifying sites for assisted colonisation

Potential AC sites were identified for all species (Table 3.5), though these vary quite drastically in terms of their size, habitat suitability and protected area coverage (Table 3.6). The White-winged Snowfinch and the Yellow-billed Chough (Figure 6) received the highest numbers of potential AC sites amongst the seven species. The Northern Tatra Mountains, located in the Western Carpathians, are predicted to be a potential AC site for four species; the remaining three species already breed in the mountains. Protected area coverage is particularly high at the site, exceeding 83% for all four species. The Northern Tatras are superior to the Low Tatras in terms of habitat suitability and protected area coverage for the White-winged Snowfinch and Yellow-billed Chough (see Figure 6 for Yellow-billed Chough sites), which both received favourable climatic projections for the two areas.

The South Scandinavian Mountains were predicted to be climatically suitable for six of the seven species under varying time periods. These mountains also often produced the most expansive potential AC sites, reaching 26 cells in the south for the Alpine Accentor. However, the lack of grassland habitat, which is of major breeding importance to the Alpine Accentor and Water Pipit, makes the Scandinavian Mountains less favourable as a potential AC site for these two species. In contrast, the Mountain range was far more favourable for the White-winged Snowfinch, a higher alpine breeding species. This is particularly apparent in the central/northern part of the mountain range where over 1,180km^2 of potentially suitable breeding habitat is available. The Scandinavian Mountains were also of high habitat suitability for the Bearded Vulture (Table 3.6), which is projected to have the smallest range of the seven species in Europe by 2080 under both dispersal scenarios (Figure 3.4). Colonisation of this site could offset the range size loss for the species by 3.5%, with potential room for expansion in the distant future as an additional six cells are projected to become climatically suitable in the distant-future (Table 3.5).

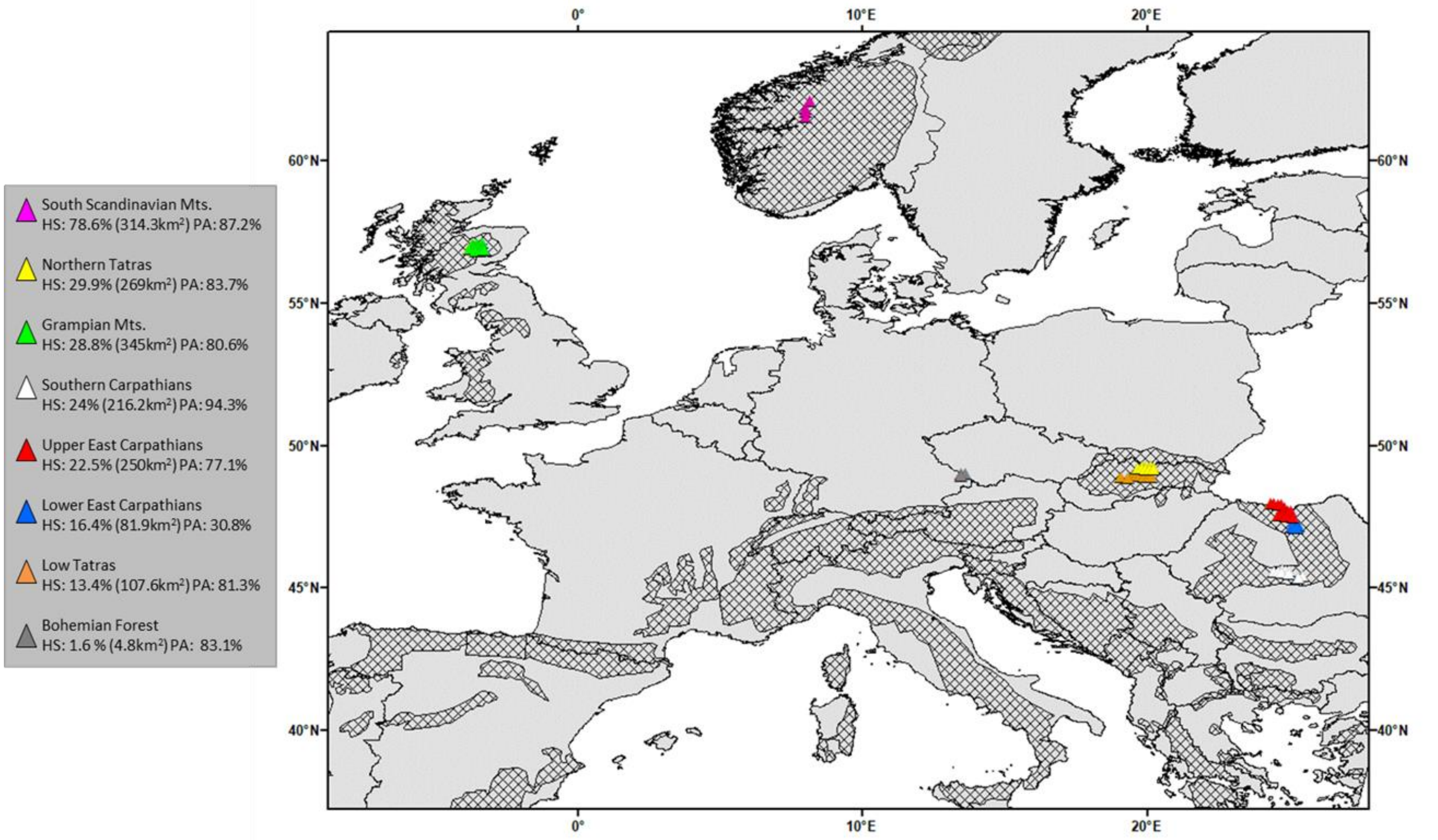

Figure 3.5 Potential assisted colonisation (AC) sites in Europe for the Yellow-billed Chough *Pyrrhocorax graculus*. HS = Habitat suitability, PA = Protected area coverage. HS represents the proportion of the total area of the climatically suitable cells (10 x 10km) containing suitable habitat. PA coverage represents the proportion of suitable habitat at each site that is protected under the Natura 2000 network (or Nationally Designated Areas for sites outside the EU). See Appendix 7 for AC site maps of the other six species.

Table 3.5 Potential assisted colonisation (AC) sites identified using climate based species distribution models. Groups of 10 x 10km cells are deemed potential AC sites if they remained uncolonized during the dispersal simulations and consist of ≥3 cells which are within the mean (+SD) Euclidean distance of the species' natal dispersal estimate of each other. 'Current' represents cells that are projected to be climatically suitable during the 1960-1990 time period. 'Near-future' represents cells that are projected to become climatically suitable under the RCA30 regional circulation model driven by the ECHAM5 general circulation model and based on the A1b emission scenario for the 2021-2050 time period. 'Distant-future' represents cells that are projected to become climatically suitable under the aforementioned climate change scenario (RCA30/ECHAM5/A1b) for the 2051-2080 time period. A potential AC site is made up of cells that are projected to be suitable between the Current and Distant-future time period and the Near-future and Distant-future time period. The cells in the final column that become suitable in the Distant-future only, are considered expansive potential cells i.e. cells within the mean (+SD) Euclidean distance of the AC site that could potentially be used by the species in the distant future.

Species	**AC site location**	**Number of suitable cells maintained between varying time periods**		Potential AC site cells	Number of cells emerging as suitable in Distant-future
		Current to Distant-future	Near-future to Distant-future		
Alpine Accentor	Central/Upper South Scandinavian Mts.	4	13	17	6
	Central/Lower South Scandinavian Mts.	4	0	4	4
	Lower South Scandinavian Mts.	2	24	26	20
	Grampian Mts.	3	0	3	0
Bearded Vulture	Northern Tatras (Western Carpathians)	4	0	4	0
	South Scandinavian Mts.	0	11	11	6
Citril Finch	Bohemian Forest	6	1	7	0
	Northern Tatras (Western Carpathians)	3	1	4	0
Rufous-tailed Rockthrush	Bohemian Forest	1	4	5	0
	Lower South Scandinavian Mts.	0	9	9	22
Water Pipit	Cambrian Mts.	0	5	5	17
	Grampian Mts.	13	0	13	0
	South Scandinavian Mts.	4	0	4	2
White-winged Snowfinch	Bohemian Forest	3	0	3	0
	Northern Tatras (Western Carpathians)	5	0	5	0
	Low Tatras (Western Carpathians)	5	0	5	0
	Upper Eastern Carpathians	3	0	3	0
	Central/Upper South Scandinavian Mts.	0	16	16	1
	Lower South Scandinavian Mts.	5	0	5	1
Yellow-billed Chough	Bohemian Forest	3	0	3	0
	Northern Tatras (Western Carpathians)	9	0	9	0
	Low Tatras (Western Carpathians)	8	0	8	0
	Upper Eastern Carpathians	14	0	14	0

	Lower Eastern Carpathians	5	0	5	0
	Southern Carpathians	9	0	9	0
	Grampian Mts.	12	0	12	0
	South Scandinavian Mts.	0	4	4	0

Table 3.6 Assessment of potential assisted colonisation (AC) sites. Groups of 10 x 10km cells that are predicted to be suitable by the SDMs under 'Current' or 'Near-future' time periods and remain suitable until the end of the 'Distant-future' time period are presented. All 'Near-future' cells are predicted suitable under the RCA30 regional circulation model driven by the ECHAM5 general circulation model and based on the A1b emission scenario. Habitat suitability represents the proportion of the total area of the climatically suitable cells containing suitable habitat. Sites with a suitable habitat composition consisting of less than 5% of habitat considered of 'major importance' for the breeding of a species are greyed out. Protected area coverage represents the proportion of suitable habitat at each site that is protected under the Natura 2000 network (or Nationally Designated Areas (CDDA) for sites outside the EU).

Species	AC site location	Total number of climatically suitable 10 x 10km cells	Habitat suitability	Protected area coverage
Alpine Accentor	Central/Upper South Scandinavian Mts.	17		
	Central/Lower South Scandinavian Mts.	4		
	Lower South Scandinavian Mts.	26		
	Grampian Mts.	3	11% (33.1km^2)	23.7%
Bearded Vulture	Northern Tatras (Western Carpathians)	4	38.6% (154.2km^2)	99.1%
	South Scandinavian Mts.	11	80.9% (890.3km^2)	92%
Citril Finch	Bohemian Forest	7	94% (658km^2)	79.4%
	Northern Tatras (Western Carpathians)	4	58.2% (232.8km^2)	98.2%
Rufous-tailed Rockthrush	Bohemian Forest	5	40.5% (202.6km^2)	93.4%
	Lower South Scandinavian Mts.	9	3.3% (29.6km^2)	0.4%
Water Pipit	Cambrian Mts.	5	45.2% (226.1km^2)	0.6%
	Grampian Mts.	13	19.8% (258.3km^2)	74.2%
	South Scandinavian Mts.	4		
White-winged Snowfinch	Bohemian Forest	3	1.60% (4.8km^2)	83.1%
	Northern Tatras (Western Carpathians)	5	35.8% (179km^2)	93.8%
	Low Tatras (Western Carpathians)	5	11% (55km^2)	78.5%
	Upper Eastern Carpathians	3	44% (132km^2)	99.8%
	Central/Upper South Scandinavian Mts.	16	74.1% (1,186.1km^2)	62%
	Lower South Scandinavian Mts.	5	68.1% (317.8km^2)	68.1%

Yellow-billed Chough	Bohemian Forest	3	1.6% (4.8km^2)	83.1%
	Northern Tatras (Western Carpathians)	9	29.9% (269km^2)	83.7%
	Low Tatras (Western Carpathians)	8	13.4% (107.6km^2)	81.3%
	Upper Eastern Carpathians	14	22.5% (250km^2)	77.1%
	Lower Eastern Carpathians	5	16.4% (81.9km^2)	30.8%
	Southern Carpathians	9	24% (216.2km^2)	94.3%
	Grampian Mts.	12	28.8% (345km^2)	80.6%
	South Scandinavian Mts.	4	78.6% (314.3km^2)	87.2%

Identifying source populations for assisted colonisation

The highest level of climatic niche overlap was most commonly observed between conditions present in the Alps and potential AC sites, though the amount of overlap varied substantially. Of the eighteen sites which underwent climate niche comparisons, the Alps had the highest amount of overlap with seven (Table 3.7). The Northern Tatras, which is a potentially favourable AC site for the White-winged Snowfinch and Yellow-billed Chough (Table 3.6, Figure 3.5), had a high level of overlap with the Alps (0.43 and 0.505 respectively, Table 3.7). The overlap was also statistically more similar than would be expected by chance for both species. Potential AC sites situated throughout the Carpathian Mountains had high levels of climatic niche overlap with alpine populations distributed in the Balkan region (Appendix 6), reaching the highest overlap for the Eastern and Southern Carpathians for the Yellow-billed Chough (Table 3.7).

The more northerly sections of the South Scandinavian Mountains tended to have the lowest levels of climatic niche overlap with current alpine populations. This was most evident for the Bearded Vulture and the South Scandinavian Mts., in which the Alps had the highest overlap value with just 0.003 (Table 3.7).

Table 3.7 Climatic niche comparisons between potential AC sites and European populations of alpine birds. European populations are grouped based on the mountain ranges they inhabit, as identified by the Global Mountain Biodiversity Assessment (Körner *et al.* 2017). The results for populations with the highest level of climatic niche overlap with each AC site are presented. AC sites that have been greyed out and do not contain niche comparison values are composed of an insufficient number of 10 x 10km cells (<5) required to run the analysis. AMK = group of mountains in the countries of Albania, Moldova and Kosovo, including Jablanica, Korab, Sar Mts., Valamara, Baba Mt. and N.E. Albanian Mts. BMG = group of mountains in the countries of Bulgaria, Macedonia and Greece, including Rila, Rhodope Mts., Pirin, Pangaion, Belasitsa Mts., Malesevske Mts., Nidze Mts. and the Osogovske Mts.
Niche similarity and equivalency significance levels: N.S. > 0.1 > . > 0.05 > * > 0.01 > ** > 0.001.

Species	AC site location	Population	Climatic niche overlap	Similarity (Population -> AC site/ AC site -> Population)	Equivalency
Alpine Accentor	Central/Upper South Scandinavian Mts.	Alps	*D* = 0.037	N.S./*	*
	Central/Lower South Scandinavian Mts.				
	Lower South Scandinavian Mts.	Southern Carpathians	*D* = 0.659	*/ *	*
	Grampian Mts.				
Bearded Vulture	Northern Tatras (Western Carpathians)				
	South Scandinavian Mts.	Alps	*D* = 0.003	N.S./N.S.	*
Citril Finch	Bohemian Forest	Alps	*D* = 0.028	N.S./N.S.	*
	Northern Tatras (Western Carpathians)				
Rufous-tailed Rockthrush	Bohemian Forest	Central & Southern Carpathians	*D* = 0.131	**/*	*
	Lower South Scandinavian Mts.	Central & Southern Carpathians	*D* = 0.139	*/*	*
Water Pipit	Cambrian Mts.	Tras-os-montes - Cantabrians - Montes Vascos - Pyrenees	*D* = 0.013	N.S./N.S.	*
	Grampian Mts.	Black Forest	*D* = 0.264	*/**	*
	South Scandinavian Mts.				
White-winged Snowfinch	Bohemian Forest				
	Northern Tatras (Western Carpathians)	Alps	*D* = 0.43	**/**	*
	Low Tatras (Western Carpathians)	Alps	*D* = 0.246	./**	*
	Upper Eastern Carpathians				
	Central/Upper South Scandinavian Mts.	Alps	*D* = 0.007	N.S./*	*
	Lower South Scandinavian Mts.	Alps	*D* = 0.001	N.S./*	*
Yellow-billed Chough	Bohemian Forest				
	Northern Tatras (Western Carpathians)	Alps	*D* = 0.505	**/**	*
	Low Tatras (Western Carpathians)	Alps	*D* = 0.215	N.S./*	*
	Upper Eastern Carpathians	BMG	*D* = 0.311	*/**	.
	Lower Eastern Carpathians	BMG	*D* = 0.273	*/*	N.S

	Southern Carpathians	AMK	$D = 0.069$	N.S./*	*
	Grampian Mts.	Alps	$D = 0.022$	N.S./*	*
	South Scandinavian Mts.				

3.4 Discussion

Studies focusing on alpine birds have been relatively scarce compared to those focusing on lowland species in farmland and forest habitats (EEA 2010; Chamberlain *et al.* 2012). However, recent research in Europe has detected upslope shifts and declines in population sizes for montane species (Lehikoinen *et al.* 2014; Flousek *et al.* 2015), particularly those at the highest altitudes (e.g. Water Pipit, Flousek *et al.* 2015). Previous European studies that have incorporated (or focused on) alpine species have either been broad and at coarse resolutions (e.g. Huntley *et al.* 2008; Barbet-Massin *et al.* 2012) or highly localised, often in one country (e.g. Maggini *et al.* 2014) or in one mountain range (e.g. Chamberlain *et al.* 2016). I projected future distributions at the European scale, but at a finer resolution in order to improve the representation of the heterogeneous climatic conditions present in mountain systems (e.g. Scherrer *et al.* 2011). My results suggest that alpine bird species will substantially decrease in range extent and disappear from many southerly distributed mountain ranges in Europe under climate change. These results are in line with those of Sekercioglu *et al.* 2008, who predicted that many mountain bird species of no current conservation concern would be threatened in the future. Constraints to their dispersal are likely to prevent European alpine birds from colonising climatically suitable sites further north, which presents an opportunity for assisted colonisation.

Dispersal limitation

One of the critical shortcomings of most existing SDMs is their consideration of only two extreme dispersal scenarios, null or unlimited (Thuiller *et al.* 2008; Bateman *et al.* 2013). Dispersal limitation is particularly important when establishing whether or not a species will require assistance in order to colonise areas of suitable climate. The ‘limited’ dispersal scenario in the present study followed a similar approach to Barbet-massin *et al.* 2012, in which the natal dispersal estimates of phylogenetically closely related species with sufficient ringing data were used as a proxy. Barbet-massin *et al.* 2012 modelled the future distributions of 409 European bird species and found that for the majority (75%), the limited dispersal scenario reduced their future distributions by less than 5% compared with the unlimited scenario. In contrast, the focal species of the present study had their potential future distributions reduced by an average of 19.6% (±

6.4%) for the limited scenario. This large proportional difference between the two dispersal scenarios elucidates the fact that there are areas of suitable climate emerging in Europe for these alpine species, they just may not be able to colonise them without assistance. This large difference is partly explained by the patchiness of the newly emerging suitable climates, in line with Europe's fragmented mountain topography. For example, the southern boundary line of the Scandinavian Mountains (based on GMBA criteria), which is projected to be climatically suitable for the White-winged Snowfinch, is more than 1000km from the nearest breeding population of this species located in the Vosges Mountains. There are no mountains located in between these two areas which could act as a stepping stone, making natural colonisation highly unlikely.

Stepping stones and corridors are often cited as important connectivity tools for enhancing species' climate change adaptation (Heller & Zavaleta 2009; Mawdsley *et al.* 2009; Hannah *et al.* 2014), by aiding dispersal through fragmented landscapes to new areas of suitable habitat and climate. However, in the case of European alpine species at the landscape scale, these approaches lose their viability due to the expansive lowlands that separate much of the unoccupied suitable climates from current distributions. This puts alpine species at a comparative disadvantage as the less contentious conservation actions that are regularly proposed for climate change mitigation (e.g. stepping stones and corridors) are not feasible at the spatial extent required for them to track their climatic niches.

It is possible that the alpine species in the present study could naturally colonise faraway unoccupied suitable climates without human assistance, through acts of vagrancy. Even relatively sedentary species, such as the Yellow-billed Chough, have been recorded considerable distances from their nearest breeding areas (Madge 2010). However, these events are rare, and their frequency is only likely to decrease (see Veit 2000) as populations are pushed upwards in elevation, reducing in numbers and increasing the distances required to make such journeys. I chose to omit acts of vagrancy from the simulations as the mechanisms that drive this somewhat random phenomenon are poorly understood (Lees & Gilroy 2009) and any inputted values would be highly speculative.

Assisted colonisation

The South Scandinavian Mountains could prove to be a future stronghold under impending climate change for five of the seven species considered in this study. This coincides with previous research which also identified the suitability of these mountains for current southerly distributed alpine birds (e.g. Smith *et al.* 2013). However, my dispersal simulations indicate that AC would be their only means of accessing this northerly mountain range. Habitat suitability assessments of the potential AC sites in the region revealed a less heterogeneous landscape than that of the current southerly distributed mountain ranges in Europe, though this would be expected based on the Scandinavian Mountains latitudinal position (Hillebrand 2004). The lack of heterogeneity, in particular the lack of alpine grassland habitat, which is of major breeding importance to the Alpine Accentor and Water Pipit (BirdLife International 2017), makes the site unsuitable for these species under current conditions. However, climate change is projected to transform the plant composition of this region (Klanderud & Birks 2003), largely at the expense of current snowbed communities (Kullman 2004; 2007). The succession of these communities into species-rich alpine grasslands is already being documented (Kullman 2010) and the hypothesis that this will continue into the future is supported by paleoecological data from the early Holocene (see Birks & Birks 2008). This would create ideal breeding habitats for the Alpine Accentor and Water Pipit, and would also benefit the White-winged Snowfinch and Yellow-billed Chough, which both utilize the habitat for foraging (Snow & Perrins 1997). If colonisation was possible, the considerable expanses of sustained suitable climates predicted to occur in this region for these four species, as well as the Bearded Vulture, could contribute towards offsetting the losses projected to take place in southern Europe.

Alpine-restricted species are regularly cited as ideal candidates for AC (Hoegh-guldberg *et al.* 2008; Loss *et al.* 2011; Thomas 2011), as they occupy climatic conditions that are predicted to disappear within their current ranges and are surrounded by unsuitable habitats that they may struggle to cross. The Yellow-billed Chough is projected to have just two populations remaining in the distant-future (by 2080) (Alps and Pyrenees), with the Pyrenean population potentially being 95.4% smaller than today. I identified seven potential AC sites in Europe for this species, the maximum of any species, with habitat suitability and protected area coverage generally being quite high. If populations were to be established at these sites, the European population would become less reliant on the Alps for sustaining species numbers. In addition, three of the potential AC sites showed the highest climatic niche overlap value with regional populations that are forecast to lose their entire climatic suitability in the distant-future (by 2080) (e.g. BMG and AMK, Appendix 4). These regional populations are situated in the Balkan Peninsula, an area that remains poorly studied phylogeographically, though genetic research on plant and invertebrate species in the region has revealed strong genetic differentiation from populations in other European Mountain ranges (Naciri & Gaudeul 2007; Theissinger *et al.* 2013; Ibrahimi *et al.* 2015; Schmitt 2017). In fact, the Alpine Accentor has a distinct subspecies endemic to the Balkan Peninsula (*Prunella collaris subalpine*). Therefore, by establishing populations through AC with individuals from BMG-BLK and AMK, any potential genetic uniqueness could be safeguarded under future climate change.

Identifying source populations

To my knowledge, the use of PCA for identifying candidate populations for AC represents a novel approach. This method is particularly applicable in situations where the distribution pattern of a species consists of isolated populations that are spread over the landscape, such as those typically restricted to mountains, islands or lakes. As climate change has altered the distributions and populations of European bird species, those species experiencing the sharpest declines possessed the lowest thermal tolerances (Jiguet *et al.* 2010). Rising temperatures can have adverse physiological effects on birds (Oswald & Arnold 2012). Therefore, AC efforts risk failure if the introduced individuals have originated from source populations with climatic regimes that are significantly different from those at the release site (Tarszisz *et al.* 2014). The use of PCA for identifying regional populations that are adapted to conditions similar to those present at AC sites represents a useful approach for conservation planning.

For temperate alpine bird species, such as those in the present study, their spatially expansive distributions provide scope for variation among the thermal tolerances of differing populations. Indeed, if there was a lack of variation, relatively similar climatic niche overlap values across the different population versus AC site comparisons would be expected, but this was not the case (see Appendix 6). If the European-wide SDMs applied in the present study averaged out the climatic niches of some locally adapted ecotypes, then these populations may not be suitable for certain AC sites. However, the subsequent use of PCA aims to overcome this issue by distinguishing between the most suitable and unsuitable populations for potential AC sites. Furthermore, by using SDMs built using spatially confined data, there is a risk of producing truncated estimations of a species' climatic niche and therefore an underestimation of its projected distribution (Thuiller *et al.* 2004; Barbet-massin *et al.* 2010).

One limitation of the PCA approach in the context of the present study is the resolution of the climate data. The resolution prevented the climatic niche comparison of smaller sized populations (<5 10 x 10km grid cells) with potential AC sites and vice versa, as the minimum sample size for the comparison is five. It is therefore possible that some of these smaller populations could be occupying climatic niches more similar to the AC sites than that of the population which we identified as having the highest level of overlap. However, a finer resolution than the one applied here would not be appropriate for modelling species at the European scale.

Additional key considerations

There are a selection of AC decision frameworks available to practitioners (e.g. Hoegh-Guldberg *et al.* 2008; Richardson *et al.* 2009; Pérez *et al.* 2012; Schwartz *et al.* 2012) and these should be utilized in order to ensure that any AC attempt is supported by transparent, systematic planning that takes into account the potential ecological and socio-economic ramifications of assisting species in their colonisation of novel environments. The focus of this study was predominantly on site selection, but there are additional species-specific considerations that must be thoroughly examined before an AC site could be deemed suitable. For example, Citril Finch populations in the northern and eastern sections of the species range overwinter in the Massif Central, the Cevennes and in the southern and western Alps (Dejonghe 1991; Marki & Adamek 2013). The average distance to wintering areas for the species is about 400–500 km (Cramp and Perrins 1994), but if a population was to be established in the Northern Tatras, which was identified as a potential AC site (Table 3.5), distances of potentially double that amount could be required to reach the wintering grounds. Similarly, without the instalment of feeding stations, the Bearded Vulture is reliant on the carcass remains of medium sized ungulates (Margalida *et al.* 2009) that are left by large predators such as wolves and Golden Eagles (Ferguson-Lees & Christie 2001). If these types of species-specific considerations are not accounted for, the success of the AC attempt could be severely jeopardised.

Conclusion

This study highlights how climate change will impact the future distributions of European alpine birds, and how assisted colonisation (AC) could mitigate these impacts. The results indicate large-scale declines in climatic space for Europe’s alpine birds, findings which are in line with those of Sekercioglu *et al.* (2008), who predicted that many mountain bird species of no current conservation concern would be threatened in the future. Populations situated in Europe’s southerly distributed mountain ranges (e.g. Iberia, Balkan Peninsula) are of particular conservation concern, as these are projected to undergo the largest decreases. Data on population numbers and trends is poor for the majority of alpine bird populations in Europe (BirdLife International 2016), though especially on the Balkan Peninsula, which is where losses are projected to be greatest. Improved monitoring should be a priority, as this could help to determine when and what intervention is required. If AC is considered, then the results presented here identify suitable recipient sites for the majority of alpine species. The exception was the Alpine Accentor, due to a lack of suitable habitat elsewhere. The Alps was the most commonly proposed source population for AC sites based on the results of climatic niche comparisons, however, a number of populations at the greatest risk from climate-induced extinction (e.g.

Balkan populations of Yellow-billed Chough) also received favourable PCA results. Future research that aims to assess the effectiveness of PCA for identifying suitable source populations is recommended, and should focus on the source localities of individuals from past translocations and their subsequent survival at release sites.

Chapter 4

Overall Discussion, Recommendations & Conclusion

4.1 Discussion

Climate change is a major threat to temperate montane bird species. Throughout temperate montane regions, indication of species' responses to climate change is beginning to emerge (Maggini *et al.* 2011; Tingley *et al.* 2012; Flousek *et al.* 2015). In Europe, climate-induced declines of montane species have already been reported (Lehikoinen *et al.* 2014; Flousek *et al.* 2015), with species restricted to the highest altitudes suffering the largest declines (Flousek *et al.* 2015). These ongoing declines highlight the importance of assessing the feasibility of a range of potential management options in the face of climate change. In this section of the thesis, I discuss the findings of my work in relation to my original research questions and recommend areas for future work.

Based on the literature reviewed (Chapter 2), it is evident that traditional biodiversity management strategies that aim to protect specific species assemblages within protected areas may lose their effectiveness under climate change (Araujo *et al.* 2004; Hannah *et al.* 2007). There is a need for more flexible management strategies that acknowledge the dynamic nature of climate change. This does not mean the abandonment of traditional approaches, rather, a combination of modifying existing management approaches (e.g. managing protected areas and improving connectivity, Gross *et al*. 2016) in addition to the deployment of new ones (e.g. assisted colonisation (AC) and targeted gene flow (TGF), Hoegh-guldberg *et al.* 2008; Macdonald *et al.* 2017) (Aim 1a).

Despite the apparent similarities in the threats faced by montane birds under climate change (see Figure 1.1), there is no 'one strategy suits all' approach to their conservation. Mountains of the temperate region are diverse, as are the bird species that rely upon them. Nonetheless, these species share certain traits (Foden *et al.* 2013) that make them more vulnerable to climate change. For example, species with preferences for altitudinal habitats close to mountain peaks (e.g. Rosy Finches and Snowfinches), or with distributions situated in lower altitudinal mountains closer to the equator (e.g. Caspian Snowcock *Tetraogallus caspius*) will be particularly vulnerable to the changing climate (Foden *et al.* 2013). The possession of such traits provides indication of a species' vulnerability; this can be used to assess the feasibility of different management strategies.

In order for conservation practitioners to make more informed decisions on the most appropriate strategy for their focal species, there is a need for future research and data collection, particularly from a dispersal and genetic perspective. I outlined the key research needs relating to protected area (PA) management, AC and TGF that will allow practitioners to better assess the most suitable approach for their focal montane species in the final section of Chapter 2 (Aim 1b).

For the seven European alpine species which formed the focus of Chapter 3, extensive declines in climatically suitable area (57-80%) are predicted to occur by 2080. Populations distributed in Europe's more southerly distributed mountain ranges are forecast to undergo the largest decreases, with many populations projected to lose their entire climatic space (Aim 2a). The deployment of conservation actions focusing on protected area management or connectivity enhancement alone are unlikely to solely suffice in preventing these declines, as suitable climatic conditions are projected to disappear entirely from species' current ranges. For the majority of European alpine species, AC could offset a proportion of these declines, as sites containing suitable habitat and PA coverage are available elsewhere (Aim 2a & c). However, the identification of suitable sites may not be possible for all species in temperate mountainous regions outside of Europe, as their specialised habitat requirements will not necessarily be replicated elsewhere (Aim 1a).

TGF represents an alternative strategy for species that meet certain criteria, specifically, a geographical distribution pattern that allows for sufficient genetic diversity and adaptation to occur (Sgro *et al.* 2011; Macdonald *et al.* 2017). The Alpine Accentor, which was not a candidate for AC, could potentially benefit from TGF, as this species exhibits the type of distribution pattern (multiple populations spread over the landscape) which may harbour isolated populations that possess the adaptive variation suited to future climate conditions in populations elsewhere. Macdonald *et al.* 2017 highlighted the usefulness of peripheral isolate populations within a species' distribution, and the Alpine Accentor has a distinct subspecies (*Prunella collaris subalpine*) restricted to the Balkan Peninsula. Southerly distributed populations inhabiting the Pindus Mountains or Peloponnese Mountains of the Balkan Peninsula may harbour the genetic variation necessary to bolster populations in other parts of the species' European range for future climate conditions.

Areas of suitable climate beyond each species' estimated dispersal capability were identified for all seven alpine species (Aim 1b). However, the dispersal data used in my study was only available for 75 common breeding species from Britain, so following Barbet-massin *et al.* (2012), I assumed that values of phylogenetically closely related species would provide reasonable estimates for the alpine species in the present study (see Appendix 2 Table A2.1). This is a realistic assumption given that for the 75 species with dispersal estimates in Paradis *et al.* (1998), phylogenetically closely related species had very similar values. Nonetheless, it is possible that the proxy dispersal estimates applied to the alpine species could be underestimations or overestimations of their actual dispersal capability, thus future distributions could be larger or smaller than the ones predicted and species may be able to colonise certain mountain ranges without human assistance. Despite this, these dispersal estimates provide a significantly more realistic scenario than the alternative ‘unlimited’ and ‘null’ dispersal scenarios that have generally been applied to SDMs in the past (Bateman *et al.* 2013).

The PCA-env method outlined by Broennimann *et al.* (2012) was used for the novel purpose of identifying the most suitable source populations for potential AC sites. By comparing the climatic conditions between the ranges of existing populations and those of potential AC sites, I determined which population may be the best adapted to site conditions (Aim 3a). Ensuring the chances of survival for introduced individuals are maximized during an AC attempt is paramount (IUCN 2013), and identifying the most climatically adapted individuals is an important first step in determining source population candidacy. However, there are a number of additionally important considerations relevant to source population candidacy that are not addressed in Table 3.7 (e.g. extinction risk and genetic diversity, Pérez *et al.* 2012; IUCN 2013). Considering these factors as well as the level of climatic niche overlap between a population and AC site is recommended. If genetic diversity can be preserved through AC without jeopardising the survival prospects of the individuals being moved, then opting for the translocation of more vulnerable populations that still have comparably high overlap may be the more favourable option, particularly when they are at high risk of extinction. For example, the Balkan populations (e.g. BMG and AMK) of the White-winged Snowfinch and Yellow-billed Chough, which are projected to lose their entire climatic space (Appendix 4) and originate from a region with high genetic differentiation from the rest of Europe (e.g. Naciri & Gaudeul 2007; Theissinger *et al.* 2013; Ibrahimi *et al.* 2015; Schmitt 2017), might be a better choice for AC sites in the Low Tatras. Furthermore, these Balkan populations may possess adaptive traits that could be preserved for use in future conservation approaches (e.g. TGF, Sgro *et al.* 2011; Macdonald *et al.* 2017).

4.2 Recommendations for future work

Data coverage

In parts of Europe, biological recording and monitoring is increasing in intensity and “citizen science” schemes where volunteers are encouraged to submit records of species they have observed are increasing in popularity. Indeed, much of this thesis would not have been possible without the citizen science schemes of GBIF and eBird. However, regional biases in spatial data coverage exist within these citizen science datasets. In Europe, there is a bias towards western countries, with high data coverage for montane species in countries such as Spain, France and Switzerland, but low data coverage in Central and Eastern European countries. The mountain ranges of Eastern Europe (e.g. Dinaric Alps, Balkan Mts., Pindus Mts. etc.) make up a substantial proportion of montane bird species' current distributions in Europe and improved occurrence data would allow for more accurate future distribution projections, which in turn could lead to more robust conservation planning. This is especially important given the high level of vulnerability detected for montane birds in the Balkan region (see Chapter 3; Appendix 4).

In addition to the aforementioned citizen science schemes, there is a need for more systematic long-term monitoring of montane bird populations across broad areas, i.e. entire mountain ranges as opposed to specific sites (Chamberlain *et al.* 2012). In Europe, I recommend particular coverage improvement in the Balkan region, where data is poor (e.g. BirdLife International 2015) and climate change vulnerability is high. Long term data on montane bird population trends would provide conservation practitioners with a gauge on when actions, such as assisted colonisation, would be required. Without monitoring schemes put in place, the declines of montane bird populations could go unnoticed, and reach a point where there are too few individuals remaining within populations for effective conservation action (e.g. AC or TGF) to take place.

Dispersal

A species' dispersal capability is considered to be one of the fundamental mechanisms that will allow it to persist under climate change (Berg *et al.* 2010). Despite the clear importance of dispersal, accurate estimates over large spatial extents remain elusive for many bird species. This is evident in the present study, in which the natal dispersal estimates of phylogenetically closely related species from research dating back almost two decades were used as a proxy for European alpine birds (Paradis *et al.* 1998). However, there are networks of ringing groups throughout Europe, many of which share their data with EURING; this data could be used to estimate the dispersal of bird species at the continental scale. For montane species, these dispersal estimates would provide insightful information on the exchange of species units between mountain ranges. Dispersal estimates have important implications for choosing the most appropriate management strategy under climate change (e.g. determining the necessity of AC). Both improved data and a greater understanding of the processes that drive dispersal, particularly over larger distances, would be valuable for determining a species adaptive capacity under future climate change and could inform the deployment of effective climate change resilient conservation strategies.

Testing PCA

The use of the PCA-env method for identifying suitable source populations for AC would benefit from further research, specifically in terms of the quantification of climatic niche overlap. This research should focus on PCA's capability of distinguishing between the successes and failures of past translocation attempts. Does a lower overlap value between the climates of a recipient site and source population correspond to a lower chance of survival, and does a higher niche overlap correspond to a higher chance of survival? By analysing the climatic variables of past translocation data, there is scope for determining what constitutes 'high' and 'low' overlap and their subsequent meaning for the survival of introduced individuals. This information would be valuable to conservation practitioners who are considering the suitability of AC for their focal species or population.

4.3 Conclusion

This thesis highlights the perilous situation that climate change poses for montane bird species. Species and populations that have generally been safeguarded from the intense anthropogenic development that has decimated lowland species are now threatened by anthropogenic climate change. Those responsible for conserving these species must devise management plans that account for this fast-moving and far-reaching threat. This thesis identifies a number of management strategies at the conservation practitioner's disposal and demonstrates how they can identify the most suitable strategy for enhancing the adaptation and survival prospects of their focal montane species. However, it is important to recognise that effective planning for future conservation actions will require wider co-operation that extends beyond geopolitical boundaries. The use of alternative management strategies in the future, such as assisted colonisation, will be reliant on co-ordinated actions between non-neighbouring countries across vast distances. The threat of climate change to biodiversity is global – our response must be too.

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Appendix 1 – List of sources used as guides to remove erroneous records

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Appendix 2 – Parameterizing MigClim (dispersal simulations)

Sexual maturation for passerines is influenced by the photoperiod (the lengthening of the day) typically during their first year of life (Blüm 2012). Therefore, I assumed that all passerines could reproduce at age 1 (iniMatAge = 1), except the Yellow-billed Chough (iniMatAge = 2), for which I used research on the Red-billed Chough as a proxy (Reid *et al.* 2003). The average age of first breeding for Bearded Vultures is around 8.1 years old, though the mean age of first successful breeding is at 11.4 years (Antor *et al.* 2007). This is reflected in the iniMatAge and propaguleProd parameters (see Table A2.1).

Appendix 2 Table A2.1. Calibration parameter values used to fit dispersal constrained distribution simulations for seven European alpine bird species. Mean (+SD) natal dispersal estimates were taken from closely related species with sufficient ring recovery data (Paradis *et al.* 1998) following Barbet-Massin *et al.* (2012).

	Mean (+SD) natal dispersal estimate (km) of closely related species	**Initial mating age**	**Probability of a cell to reproduce propagules at each year, starting from year of colonisation**
Parameter:	**dispKernel**	**iniMatAge**	**propaguleProd**
Alpine Accentor	2 SD + 7 (Dunnock)	1 (Blüm 2012)	0.6
Alpine Citril Finch	11 SD + 18 (European Goldfinch)	1 (Blüm 2012)	0.6
Bearded Vulture	72 SD + 115 (-)	8 (Antor *et al.* 2007)	0.6
Rufous-tailed Rock thrush	19 SD + 29 (Northern Wheatear)	1 (Blüm 2012)	0.6
Water Pipit	25 SD + 30 (Rock Pipit)	1 (Blüm 2012)	0.6
White-winged Snowfinch	11 SD + 18 (European Goldfinch)	1 (Blüm 2012)	0.6
Yellow-billed Chough	10 SD + 13 (Carrion Crow)	2 (Reid *et al.* 2003)	0.6

For the propaguleProd parameter, I ran a sensitivity analysis to test the impact of different values on the parameter using the current distribution and future climate suitability maps of the Bearded Vulture as a case study. This species has the greatest dispersal capability and would therefore be most sensitive to changes in the propaguleProd parameter. Each dispersal simulation was run five times and the mean is presented (see Table A2.2). No change was detected between the different propaguleProd values, therefore I assumed a best-case productivity scenario in which species have a high probability of successfully producing young at their initial maturity age (see Table A2.1).

Appendix 2 Table A2.2. Sensitivity analysis results for simulating the propaguleProd parameter on the Bearded Vulture *Gypaetus barbatus.* Occupied count = Number of cells in an "occupied" state at the end of dispersal simulation – by 2080 (i.e. the potential distribution of species given the implemented dispersal restrictions). Total colonised = Total number of newly colonised cells during the entire simulation based on mean + SD natal dispersal – by 2080. Total decolonised = Total number of cells lost due to climate turning unfavourable during the entire simulation – by 2080.

Propagule prod value	Occupied count	Total colonised	Total decolonised
0.1, 0.2, 0.3, 0.5, 0.7, 0.8, 0.9	410	299	804
0.1, 0.2, 0.4, 0.8 (Antor *et al.* 2007)	410	299	804
0.1, 0.5, 0.99	410	299	804
0.1	410	299	804
0.3	410	299	804
0.5	410	299	804
0.9	410	299	804

Appendix 3 – Habitat suitability

Appendix 3 Table A3.1. Correspondence between IUCN habitat classes and CORINE Land Cover (CLC) classes. Only IUCN habitat classes that are deemed as suitable for the breeding of the seven alpine species considered in this study are presented.

IUCN habitat classification scheme		**CLC classes**	
IUCN classification no.	Land-use type	CLC classification no.	Land-use type
1	Forest	3.1.1	Broad-leaved forest
		3.1.2	Coniferous forest
		3.1.3	Mixed forest
3	Shrubland	3.2.4	Transitional woodland-shrub
		3.2.2	Moors and Heathland
3.8	Mediterranean-type Shrubby Vegetation	3.2.4	Transitional woodland-shrub
4	Grassland	2.3.1	Pastures
		3.2.1	Natural Grasslands
6	Rocky areas (e.g. inland cliffs, mountain peaks)	3.3.2	Bare rocks
		3.3.3	Sparsely vegetated areas
14	Terrestrial/artificial		
14.5	Urban areas		
		1.1.2	Discontinuous urban fabric
		1.4.1	Green urban areas
		1.4.2	Sport and leisure facilities

Appendix 3 Table A3.2. Habitat suitability based on the harmonization of the IUCN habitat classification system and the CORINE Land Cover (CLC) inventory in Appendix 3. Only land-use classes that were categorised as suitable breeding habitat for a species and that were present at one or more potential assisted colonisation sites are displayed. CLC classes denoted as 'suitable' for a species indicates that the species occurs in the habitat regularly or frequently during the breeding season. 'Major' indicates that the habitat type is important for the survival of the species, either because it has an absolute requirement for the habitat at some point in its life cycle (e.g. for breeding or as a critical food source), or it is the primary habitat (or one of two primary habitats) within which the species usually occurs or within which most individuals occur. If forests are deemed of 'major' importance to the breeding of a species, they must represent a combined >10% of the land classes at the AC site.

CLC Classes	**Species**						
	Alpine Accentor	Bearded Vulture	Citril Finch	Rufous-tailed Rock Thrush	White-winged Snowfinch	Water Pipit	Yellow-billed Chough
Discontinuous urban fabric	-	Suitable	-	-	Suitable	-	Suitable
Green urban areas	-	Suitable	-	-	Suitable	-	Suitable
Sport and leisure facilities	-	Suitable	-	-	Suitable	-	Suitable
Pastures	Suitable	Suitable	Suitable	Suitable	Suitable	Suitable	Suitable
Broad-leaved forest	-	-	Major	-	-	-	-
Coniferous forest	-	-	Major	-	-	-	-
Mixed forest	-	-	Major	-	-	-	-
Natural grasslands	Major	Suitable	Suitable	Suitable	Suitable	Major	Suitable
Transitional woodland-shrub	-	-	Suitable	Suitable	-	-	-
Bare rocks	Major	Major	-	Major	Major	Major	Major
Sparsely vegetated areas	Suitable	Suitable	-	Suitable	Suitable	Suitable	Suitable

I classed 'Discontinuous urban fabric', 'green urban areas' and 'Sports and Leisure facilities' as 'suitable' for the White-winged Snowfinch, despite Terrestrial/artificial areas not being recognised as suitable in the species' Red List habitat suitability table. This decision was made because there is clear mention of the species' association with urban habitats in the text account of the species' Red List profile, as well as accounts of breeding in urban habitats given by Snow *et al.* (1997) and Rolando *et al.* (2007).

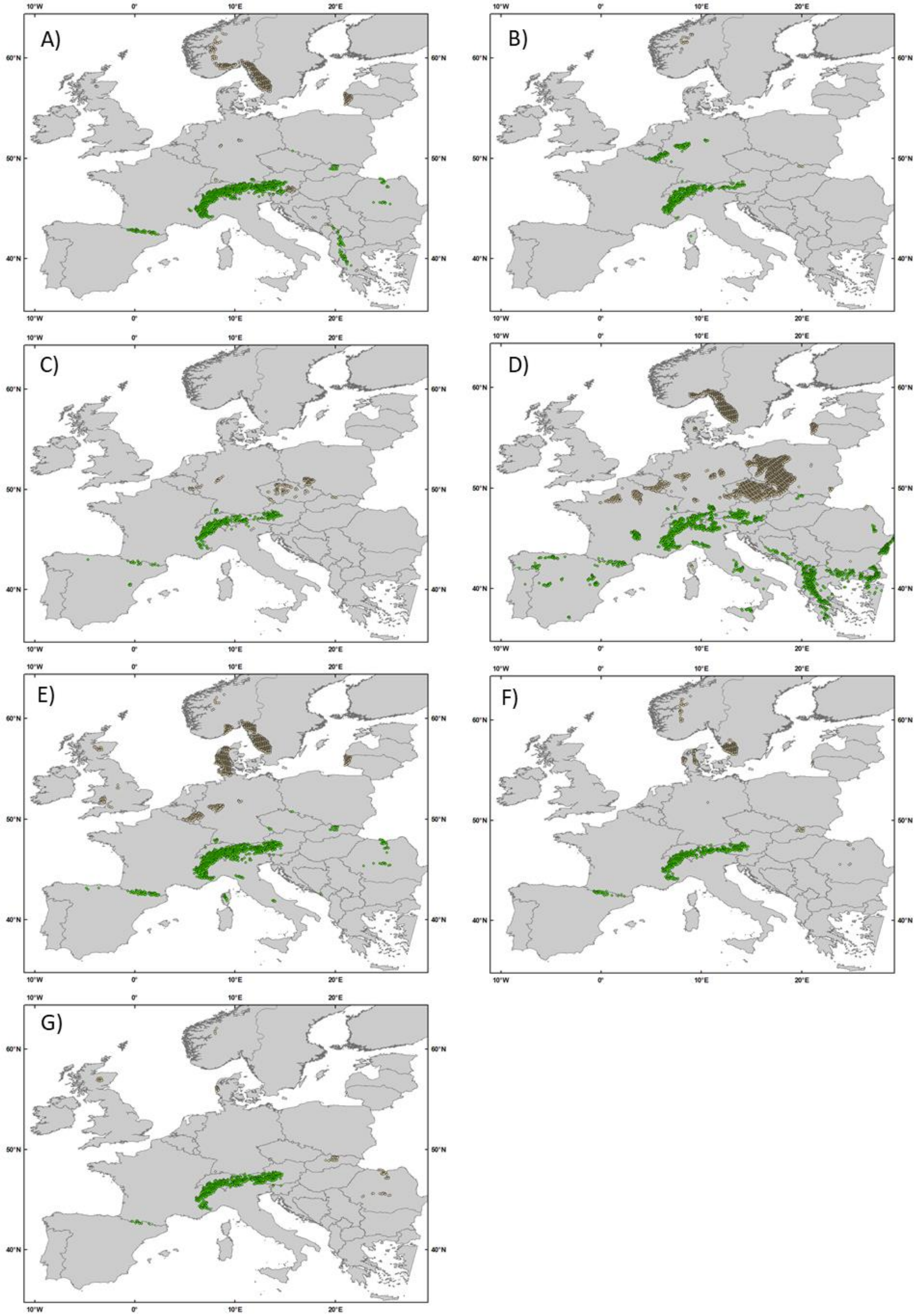
Appendix 4 – Regional population changes

Appendix 4 Table A4.1. Predicted change in areas of climatic suitability from current distribution to projected 2021-2050 (Near-future) and 2051-2080 (Distant-future) distributions for seven European alpine birds after accounting for each species mean (+SD) natal dispersal. Loss of climatically suitable area is denoted by a minus, while gain in suitable area is denoted by a plus. Populations are grouped based on their geographical location with respect to the mountain boundaries identified by the Global Mountain Biodiversity Assessment (GMBA). When a section of a species' distribution crosses multiple mountain boundary lines in a continuous fashion it is considered as one single population and is denoted by the hyphenation of multiple population abbreviations.
Population abbreviations are as follows: Sistema Betico: SIB * Sistema Central: SIC * Serra de Estrela: SDE * Tras-os-montes: TRA * Cantabrians: CAN * Monte Faro: MOF * Sistema Iberico: SII * Southeast Iberian range: SEI * Montes Vascos: MOV * Pyrenees: PYR * Corsica: COR * Sardinia: SAR * Mallorca: MAL * Massif Central: MAS * Jura Mountains: JUR * Vosges: VOS * Black Forest: BLF * European Alps: ALP * Bohemian Forest: BOH * Apennines: APN * Monte Gargano: MOG * Sicily: SCL * Dinaric Alps: DIN * Sudetes Mountains: SUD * Carpathians: CAR * Little Carpathians: L.CAR * Balkan Mountains: BLK * Rila, Rhodope Mts, Pirin, Pangaion, Belasitsa Mts, Malesevske Mts, Nidze Mts, Osogovske Mts: BMG * Pindus Mountains, Oros Othris, Olimbos, Gjere: PIN * Jablanica, Korab, Sar Mts, Valamara, Baba Mt, N.E. Albania: AMK * Peloponnese: PEL * Crete: CRE (N = North, C = Central, E = East, S = South, W = West).

Species	**Areas of current occupancy**	**Areas predicted to lose entire climatic suitability by 2050**	**Areas predicted to remain climatically suitable by 2050** (proportional change)	**Areas predicted to lose entire climatic suitability by 2080**	**Areas predicted to remain climatically suitable by 2051-2080** (proportional change)
Alpine Accentor	SIB ┃ SIC ┃CAN ┃ MOV ┃ PYR ┃MAS ┃ JUR ┃ VOS ┃ ALP ┃ APN ┃ N. DIN ┃ C. DIN ┃ SUD┃ W.CAR ┃ BMG ┃ AMK-PIN ┃S.PIN ┃ PEL	SIB┃ SIC ┃ MOV ┃MAS ┃ PEL	CAN (-84.2%)┃ PYR (-44.5%) ┃ JUR (+925%) ┃VOS (+166.7%) ┃ ALP (-1.9%) ┃APN (-80%) ┃ N.DIN (-75%) ┃ C. DIN (-71.6%) ┃ SUD (-85.7%) ┃ W.CAR (5.3%) ┃ BMG (-83.3%) ┃ AMK-PIN (-66.7%)┃ S.PIN (-88.9%)	CAN ┃ JUR┃ VOS ┃ APN ┃N.DIN ┃ BMG	PYR (-76.3%) ┃ ALP (-46.3%) ┃ C. DIN (-91%) ┃ SUD (-92.9%) ┃ W.CAR (-75.7%) ┃ AMK-PIN (-51.7%)┃ S.PIN (-66.7%)
Bearded Vulture	SIB ┃ MOV ┃ PYR ┃ COR ┃ ALP ┃CRE	SIB	┃MOV (-92.9%) ┃ PYR (-56.7%) ┃ COR (-66.7%) ┃ALP (-11.3%) ┃CRE (-87.5%)	MOV┃ PYR ┃ CRE	COR (-93.3%) ┃ALP (-48.2%)
Citril Finch	SIB ┃ SIC ┃ SEI ┃ CAN ┃ MOV ┃ SII ┃ PYR ┃ MAS ┃JUR ┃ VOS ┃ BLF ┃ ALP	SIB┃ SIC┃ SII ┃	SEI (-19.7%) ┃ CAN (-67.6%) ┃ MOV (-96.4%) ┃PYR (-31.8%) ┃ MAS (-42.6%) ┃ JUR (+165.2%) ┃ VOS (-6.3%) ┃ BLF (+105.9%) ┃ ALP (-5.6%)	MOV┃MAS┃JUR┃VOS	SEI (-94.4%) ┃CAN (-98.5%) ┃PYR (-94.3%) ┃ BLF (-64.7%) ┃ALP (-70.4%)
Rufous-tailed Rock Thrush	SIB ┃ N.SIB-SDE-SIC-TRA-CAN-SII-SEI-MOV-PYR ┃ MAL ┃ SAR ┃MAS ┃ALP-N.APN-JUR-N.DIN ┃APN-MOG ┃SCL ┃ L.CAR ┃W.CAR ┃S.CAR-C.CAR ┃ BMG-BLK ┃ DIN-	MAL ┃ SAR ┃ L.CAR	SIB (-85.6%) ┃ N.SIB-SDE-SIC-TRA-CAN-SII-SEI-MOV-PYR (-57.3%) ┃ MAS (+26.1%)┃ ALP-JUR-N.APN-VOS-BLF-N.DIN (+13.5%) ┃APN-MOG (-48.5%) ┃SCL (0%)┃W.CAR (-37.5%) ┃ S.CAR-C.CAR (-90.9%) ┃BMG-BLK (-64.3%) ┃DIN-AMK-PIN-PEL (-	S.CAR-C.CAR	SIB (-97.7%) ┃ N.SIB-SIC-TRA-CAN-SII-SEI-MOV-PYR (-92.5%)┃ MAS (-66.4%) ┃ALP-JUR-N.APN-VOS-BLF-N.DIN (-17%) ┃APN-MOG (-83.2%) ┃SCL (+500%)┃ W.CAR (0%)┃ BMG-BLK (-63.3%) ┃DIN-AMK-PIN-PEL (+25.5%)

	AMK-PIN-PEL❙		58.4%)		
Water Pipit	SIC ❙ MOF ❙ TRA-CAN-MOV-PYR ❙ SII ❙ SAR ❙ COR ❙ MAS ❙ JUR ❙VOS ❙ BLF ❙ ALP-N.DIN ❙ APN ❙BOH ❙ DIN ❙ SUD ❙ CAR ❙ AMK ❙ BLK-BMG ❙PIN	SIC❙MOF ❙SII ❙ SAR	❙TRA-CAN-MOV-PYR (-70.6%)❙ COR (-48.1%) ❙MAS (-90.9%) ❙ JUR (+2.6%) ❙VOS (-30%)❙BLF (+33.3%) ❙ ALP-N.DIN (+5.2%) ❙APN (-73.2%)❙ BOH (+77.8%) ❙DIN (-14.5%) ❙SUD (-80%)❙ CAR (-13.3%)❙AMK (+21.4%) ❙BLK-BMG (-25%)❙ PIN (-71%)	MAS❙BLF❙VOS❙AMK❙BLK-BMG❙PIN	TRA-CAN-MOV-PYR (-90.5%) ❙ COR (-63%) ❙ JUR (-98.7%) ❙BLF (-74.1%) ❙ ALP-N.DIN (-53.5%) ❙ APN (-92.3%) ❙BOH (-55.6%)❙ DIN (-99.7%) ❙ SUD (-90%) ❙ CAR (-84.9%)
White-winged Snowfinch	CAN ❙PYR ❙ MAS ❙ VOS ❙ ALP ❙APN ❙DIN ❙ AMK ❙ PIN	APN ❙PIN	CAN (-73.7%) ❙PYR (-14.5%) ❙VOS (-57.1%) ❙ALP (-18.6%)❙DIN (-88.8%) ❙ AMK (-67.9%) ❙	CAN❙MAS❙VOS❙DIN❙AMK	PYR (-86.1%) ❙ALP (-70.5%)
Yellow-billed Chough	CAN ❙MOV ❙ PYR ❙ COR ❙ APN ❙ JUR ❙ALP ❙ DIN❙BLK-BMK ❙ AMK-N.PIN ❙ S.PIN ❙ PEL ❙CRE	❙MOV ❙ APN ❙ BLK-BMG ❙ S.PIN ❙ PEL ❙ CRE	CAN (-97.2%)❙PYR (-50.5%) ❙ COR (-75%) ❙JUR (+766.7%) ❙ ALP (-12.4%) ❙ DIN (-66.7%)❙ AMK-N.PIN (-80%) ❙	CAN❙COR❙JUR❙DIN❙AMK-N.PIN	PYR (-95.4%) ❙ALP (-62.5%)

Appendix 5 - Projected future suitable climate and limited dispersal



Appendix 5 Figure A5.1. Projected suitable climate for seven European alpine birds for 2051-2080 under the RCA30 regional circulation model driven by the ECHAM5 general circulation model and based on the A1b emission scenario.

Green circles represent areas colonised by a species based on the mean + SD natal dispersal estimate (limited dispersal scenario). Cream circles represent areas that are climatically suitable, but the species was unable to colonise due to dispersal limitation. A) Alpine Accentor *Prunella collaris*, B) Bearded Vulture *Gypaetus barbatus*, C) Citril Finch *Carduelis citrinella*, D) Rufous-tailed Rock Thrush *Monticola saxatilis*, E) Water Pipit *Anthus spinoletta*, F) White-winged Snowfinch *Montifringilla nivalis*, G) Yellow-billed Chough *Pyrrhocorax graculus*.

Appendix 6 – Full Principal Components Analysis results

Appendix 6 Table A6.1. Climatic niche comparisons between European populations of the Alpine Accentor *Prunella collaris* and a potential assisted colonisation site in the Central/Upper South Scandinavian Mountains. The variation among the AC site and species populations explained by the first two axes of the PCA is also presented.

Populations	**Climatic niche overlap (D)**	**Equivalency**	**Similarity** Population → AC site	**Similarity** AC site → Population
Alps	0.037	0.0198	0.29703	0.0198
Pyrenees	0	0.0198	0.77228	0.32673
Cantabrians	0	0.0198	1	1
Sistema Betico	0	0.0198	1	1
Sistema Central	N/A*	N/A*	N/A*	N/A*
Massif Central	0	0.0198	1	1
Jura Mts.	N/A*	N/A*	N/A*	N/A*
Apennines (North)	0	0.0198	1	1
Apennines (Lower North)	N/A*	N/A*	N/A*	N/A*
Apennines (Central)	N/A*	N/A*	N/A*	N/A*
Dinaric Alps (North)	0	0.0198	1	1
Dinaric Alps (Central & South)	0	0.0198	0.65347	0.07921
AMK-North Pindus Mts.	0	0.0198	0.74257	0.26733
BMG	0	0.0198	1	1
Pindus Mts. (South)	0	0.0198	1	1
Peloponnese Mts.	N/A*	N/A*	N/A*	N/A*
Southern Carpathians	0	0.0198	0.44554	0.05941
Eastern Carpathians	0	0.0198	1	1
Western Carpathians	0.005	0.0198	0.34653	0.20792
Central Carpathians	N/A*	N/A*	N/A*	N/A*
Sudetes Mts.	0	0.0198	0.59406	0.12871
Variation	PC1	60.83%		
	PC2	25.99%		

*Test not applicable due to limited sample size.

Appendix 6 Table A6.2. Climatic niche comparisons between European populations of the Alpine Accentor *Prunella collaris* and a potential assisted colonisation site in the Lower South Scandinavian Mountains. The variation among the AC site and species populations explained by the first two axes of the PCA is also presented.

Populations	**Climatic niche overlap (D)**	**Equivalency**	**Similarity** Population → AC site	**Similarity** AC site → Population
Alps	0.144	0.0198	0.14851	0.12871
Pyrenees	0.005	0.0198	0.51485	0.40594
Cantabrians	0.001	0.0198	0.54455	0.48515
Sistema Betico	0.001	0.0198	0.36634	0.71287
Sistema Central	N/A*	N/A*	N/A*	N/A*
Massif Central	0	0.0198	0.27723	0.23762
Jura Mts.	N/A*	N/A*	N/A*	N/A*
Apennines (North)	0	0.0198	0.41584	0.52475
Apennines (Lower North)	N/A*	N/A*	N/A*	N/A*
Apennines (Central)	N/A*	N/A*	N/A*	N/A*
Dinaric Alps (North)	0.002	0.0198	0.47525	0.49505
Dinaric Alps (Central & South)	0.168	0.0198	0.20792	0.09901
AMK-North Pindus Mts.	0.237	0.0198	0.25743	0.17822
BMG	0.001	0.0198	0.20792	0.22772
Pindus Mts. (South)	0	0.0198	1	1
Peloponnese Mts.	N/A*	N/A*	N/A*	N/A*
Southern Carpathians	0.659	0.0198	0.0198	0.0198
Eastern Carpathians	0.039	0.0198	0.15842	0.09901
Western Carpathians	0.428	0.0198	0.05941	0.05941
Central Carpathians	N/A*	N/A*	N/A*	N/A*
Sudetes Mts.	0.518	0.0396	0.0297	0.07921
Variation	PC1	60.83%		
	PC2	25.99%		

*Test not applicable due to limited sample size.

Appendix 6 Table A6.3. Climatic niche comparisons between European populations of the Bearded Vulture *Gypaetus barbatus* and a potential assisted colonisation site in the Scandinavian Mountains. The variation among the AC site and species populations explained by the first two axes of the PCA is also presented.

Populations	**Climatic niche overlap (D)**	**Equivalency**	**Similarity** Population → AC site	**Similarity** AC site → Population
Alps	0.003	0.0198	0.44554	1
Pyrenees	0	0.0198	1	1
Sistema Betico	N/A*	N/A*	N/A*	N/A*
Montes Vascos	0	0.0198	1	1
Corsican Mts.	0	0.0198	1	1
Crete	0	0.0198	1	1
Variation	PC1	61.51%		
	PC2	27.7%		

*Test not applicable due to limited sample size.

Appendix 6 Table A6.4. Climatic niche comparisons between European populations of the Citril Finch *Carduelis citrinella* and a potential assisted colonisation site in the Bohemian Forest. The variation among the AC site and species populations explained by the first two axes of the PCA is also presented.

Populations	**Climatic niche overlap (D)**	**Equivalency**	**Similarity** Population → AC site	**Similarity** AC site → Population
Alps	0.028	0.0198	0.19802	0.38614
Black Forest	0	0.0198	0.31683	0.32673
Cantabrians	0	0.0198	1	1
Jura Mts.	0	0.0198	0.29703	0.32673
Massif Central	0	0.0198	1	1
Southeast Iberian	0	0.0198	0.83168	0.40594
Sistema Betico	N/A*	N/A*	N/A*	N/A*
Sistema Central	0	0.0198	1	1
Pyrenees-Montes Vascos-Sistema Iberico	0	0.0198	0.92079	0.83168
Vosges	0	0.0198	1	1

Variation	PC1	73.72%
	PC2	16.37%

*Test not applicable due to limited sample size.

Appendix 6 Table A6.5. Climatic niche comparisons between European populations of the Rufous-tailed Rock Thrush *Monticola saxatilis* and a potential assisted colonisation site in the Bohemian Forest. The variation among the AC site and species populations explained by the first two axes of the PCA is also presented.

Populations	**Climatic niche overlap (D)**	**Equivalency**	**Similarity** Population → AC site	**Similarity** AC site → Population
Alps- Apennines (North) - Jura Mts.-Dinaric Alps (North)	0.007	0.0198	0.35644	0.20792
Apennines (Central & South)-Monte Gargano	0	0.0198	0.65347	0.66337
BMG-Balkan Mts.	0.002	0.0198	0.48515	0.46535
Dinaric Alps-AMK-Pindus Mts.-Peloponnese Mts.	0.035	0.0198	0.25743	0.19802
Eastern Carpathians	0.023	0.0198	0.07921	0.11881
All of Spanish Mountains above Sistema Betico	0	0.0198	0.9604	0.62376
Little Carpathians (1)	N/A*	N/A*	N/A*	N/A*
Mallorca (2)	N/A*	N/A*	N/A*	N/A*
Massif Central	0	0.0198	0.58416	0.45545
Sardinia (3)	N/A*	N/A*	N/A*	N/A*
Southern & Central Carpathians	0.131	0.0198	0.0099	0.0297

Sistema Betico	0	0.0198	1	1
Western Carpathians	0.008	0.0198	0.17822	0.20792
Siciliy (2)	N/A*	N/A*	N/A*	N/A*
Variation	PC1	61.25%		
	PC2	22.61%		

*Test not applicable due to limited sample size.

Appendix 6 Table A6.6. Climatic niche comparisons between European populations of the Rufous-tailed Rock Thrush *Monticola saxatilis* and a potential assisted colonisation site in the Lower South Scandinavian Mountains. The variation among the AC site and species populations explained by the first two axes of the PCA is also presented.

Populations	**Climatic niche overlap (D)**	**Equivalency**	**Similarity** Population → AC site	**Similarity** AC site → Population
Alps- Apennines (North) - Jura Mts.- Dinaric Alps (North)	0.007	0.0198	0.41584	0.20792
Apennines (Central & South)-Monte Gargano	0	0.0198	0.52475	0.64356
BMG-Balkan Mts.	0.001	0.0198	0.50495	0.47525
Dinaric Alps-AMK-Pindus Mts.-Peloponnese Mts.	0.034	0.0198	0.18812	0.13861
Eastern Carpathians	0.012	0.0198	0.09901	0.21782
All of Spanish Mountains above Sistema Betico	0	0.0198	0.75248	0.60396
Little Carpathians (1)	N/A*	N/A*	N/A*	N/A*
Mallorca (2)	N/A*	N/A*	N/A*	N/A*
Massif Central	0.001	0.0198	0.30693	0.22772
Sardinia (3)	N/A*	N/A*	N/A*	N/A*
Southern & Central Carpathians	0.139	0.0396	0.0198	0.0396
Sistema Betico	0	0.0198	0.47525	0.67327
Western Carpathians	0.01	0.0198	0.23762	0.37624
Siciliy (2)	N/A*	N/A*	N/A*	N/A*
Variation	PC1	61.58%		
	PC2	25.5%		

*Test not applicable due to limited sample size.

Appendix 6 Table A6.7. Climatic niche comparisons between European populations of the Water Pipit *Anthus spinoletta* and a potential assisted colonisation site in the Cambrian Mountains. The variation among the AC site and species populations explained by the first two axes of the PCA is also presented.

Populations	**Climatic niche overlap (D)**	**Equivalency**	**Similarity** Population → AC site	**Similarity** AC site → Population
Alps-Dinaric Alps (North)	0	0.0198	0.62376	0.70297
AMK	0	0.0198	1	1
Apennines (North)	0	0.0198	0.48515	0.26733
Apennines (Central)	0	0.0198	0.57426	0.74257
Apennines (South)	0	0.0198	1	1
Black Forest	0	0.0198	0.47525	0.06931
BMG + Balkan Mts.	0	0.0198	1	1
Bohemian Forest	0	0.0198	1	1
Pyrenees-Montes Vascos-Cantabrians-Tras-os-montes	0.013	0.0198	0.23762	0.31683
Central Carpathians	0	0.0198	1	1
Eastern Carpathians	0	0.0198	1	1
Southern Carpathians	0	0.0198	1	1
Western Carpathians	0	0.0198	1	1
Corsican Mts.	0.005	0.0198	0.13861	0.05941
Dinaric Alps	0	0.0198	0.66337	0.20792
Jura Mts.	0	0.0198	1	1
Massif Central	0	0.0198	1	1
Monte Faro	N/A*	N/A*	N/A*	N/A*
Pindus Mts.	0	0.0198	1	1
Sardinia	N/A*	N/A*	N/A*	N/A*
Sistema Central	0	0.0198	1	1
Sistema Iberico	0	0.0198	1	1
Sudetes	0	0.0198	1	1
Vosges	0	0.0198	1	1
Variation	PC1	57.58%		
	PC2	24.39%		

*Test not applicable due to limited sample size.

Appendix 6 Table A6.8. Climatic niche comparisons between European populations of the Water Pipit *Anthus spinoletta* and a potential assisted colonisation site in the Grampian Mountains. The variation among the AC site and species populations explained by the first two axes of the PCA is also presented.

Populations	**Climatic niche overlap (D)**	**Equivalency**	**Similarity** Population → AC site	**Similarity** AC site → Population
Alps-Dinaric Alps (North)	0.035	0.0198	0.19802	0.07921
AMK	0	0.0198	0.73267	0.37624
Apennines (North)	0.005	0.0198	0.44554	0.27723
Apennines (Central)	0	0.0198	0.47525	0.16832
Apennines (South)	0	0.0198	1	1
Black Forest	0.264	0.0198	0.0297	0.0099
BMG + Balkan Mts.	0	0.0198	1	1
Bohemian Forest	0	0.0198	1	1

Pyrenees-Montes Vascos-Cantabrians-Tras-os-montes	0.068	0.0198	0.22772	0.07921
Central Carpathians	0	0.0198	1	1
Eastern Carpathians	0	0.0198	1	1
Southern Carpathians	0	0.0198	0.66337	0.42574
Western Carpathians	0	0.0198	0.57426	0.74257
Corsican Mts.	0.001	0.0198	0.27723	0.27723
Dinaric Alps	0.018	0.0198	0.44554	0.06931
Jura Mts.	0.034	0.0198	0.12871	0.0495
Massif Central	0.002	0.0198	0.28713	0.11881
Monte Faro	N/A*	N/A*	N/A*	N/A*
Pindus Mts.	0	0.0198	0.74257	0.44554
Sardinia	N/A*	N/A*	N/A*	N/A*
Sistema Central	0	0.0198	1	1
Sistema Iberico	0	0.0198	1	1
Sudetes	0	0.0198	0.59406	0.55446
Vosges	0.019	0.0198	0.16832	0.0495
Variation	PC1	57.96%		
	PC2	25.07%		

*Test not applicable due to limited sample size.

Appendix 6 Table A6.9. Climatic niche comparisons between European populations of the Water Pipit *Anthus spinoletta* and a potential assisted colonisation site in the South Scandinavian Mountains. The variation among the AC site and species populations explained by the first two axes of the PCA is also presented.

Populations	**Climatic niche overlap (D)**	**Equivalency**	**Similarity** Population → AC site	**Similarity** AC site → Population
Alps-Dinaric Alps (North)	0.003	0.0198	0.55446	0.0396
AMK	0	0.0198	0.84158	0.22772
Apennines (North)	0	0.0198	1	1
Apennines (Central)	0	0.0198	1	1
Apennines (South)	0	0.0198	1	1
Black Forest	0	0.0198	1	1
BMG + Balkan Mts.	0	0.0198	1	1
Bohemian Forest	0	0.0198	1	1
Pyrenees-Montes Vascos-Cantabrians-Tras-os-montes	0	0.0198	1	1
Central Carpathians	0	0.0198	1	1
Eastern Carpathians	0	0.0198	1	1
Southern Carpathians	0	0.0198	0.70297	0.06931
Western Carpathians	0	0.0198	0.55446	0.16832
Corsican Mts.	0	0.0198	1	1
Dinaric Alps	0	0.0198	1	1
Jura Mts.	0	0.0198	0.86139	0.63366
Massif Central	0	0.0198	1	1
Monte Faro	N/A*	N/A*	N/A*	N/A*
Pindus Mts.	0	0.0198	1	1
Sardinia	N/A*	N/A*	N/A*	N/A*

Sistema Central	0	0.0198	1	1
Sistema Iberico	0	0.0198	1	1
Sudetes	0	0.0198	0.66337	0.07921
Vosges	0	0.0198	1	1
Variation	PC1	57.62%		
	PC2	28.63%		

*Test not applicable due to limited sample size.

Appendix 6 Table A6.10. Climatic niche comparisons between European populations of the White-winged Snowfinch *Montifringilla nivalis* and a potential assisted colonisation site in the Central/Upper South Scandinavian Mountains. The variation among the AC site and species populations explained by the first two axes of the PCA is also presented.

Populations	**Climatic niche overlap (D)**	**Equivalency**	**Similarity** Population → AC site	**Similarity** AC site → Population
Alps	0.007	0.0198	0.52475	0.0297
Pyrenees	0	0.0198	0.82178	0.30693
Cantabrians	0	0.0198	1	1
Massif Central	N/A*	N/A*	N/A*	N/A*
Vosges	0	0.0198	1	1
Apennines (Central)	0	0.0198	1	1
Dinaric Alps	0	0.0198	0.89109	0.82178
AMK	0	0.0198	0.78218	0.23762
Pindus Mts. (North)	N/A*	N/A*	N/A*	N/A*
Variation	PC1	58.56%		
	PC2	27.31%		

*Test not applicable due to limited sample size.

Appendix 6 Table A6.11. Climatic niche comparisons between European populations of the White-winged Snowfinch *Montifringilla nivalis* and a potential assisted colonisation site in the Lower South Scandinavian Mountains. The variation among the AC site and species populations explained by the first two axes of the PCA is also presented.

Populations	**Climatic niche overlap (D)**	**Equivalency**	**Similarity** Population → AC site	**Similarity** AC site → Population
Alps	0.001	0.0198	0.47525	0.0198
Pyrenees	0	0.0198	1	1
Cantabrians	0	0.0198	1	1
Massif Central	N/A*	N/A*	N/A*	N/A*
Vosges	0	0.0198	1	1
Apennines (Central)	0	0.0198	1	1
Dinaric Alps	0	0.0198	1	1
AMK	0	0.0198	0.65347	0.22772
Pindus Mts. (North)	N/A*	N/A*	N/A*	N/A*

Variation	PC1	58.56%
	PC2	27.31%

*Test not applicable due to limited sample size.

Appendix 6 Table A6.12. Climatic niche comparisons between European populations of the White-winged Snowfinch *Montifringilla nivalis* and a potential assisted colonisation site in the Northern Tatras (Western Carpathians). The variation among the AC site and species populations explained by the first two axes of the PCA is also presented.

Populations	**Climatic niche overlap (D)**	**Equivalency**	**Similarity** Population → AC site	**Similarity** AC site → Population
Alps	0.479	0.0396	0.0099	0.0099
Pyrenees	0.115	0.0198	0.34653	0.12871
Cantabrians	0.002	0.0198	0.9505	0.61386
Massif Central	N/A*	N/A*	N/A*	N/A*
Vosges	0.009	0.0198	0.46535	0.24752
Apennines (Central)	0	0.0198	0.77228	0.61386
Dinaric Alps	0.033	0.0198	0.40594	0.23762
AMK	0.03	0.0198	0.58416	0.27723
Pindus Mts. (North)	N/A*	N/A*	N/A*	N/A*
Variation	PC1	60.79%		
	PC2	19.76%		

*Test not applicable due to limited sample size.

Appendix 6 Table A6.13. Climatic niche comparisons between European populations of the White-winged Snowfinch *Montifringilla nivalis* and a potential assisted colonisation site in the Low Tatras (Western Carpathians). The variation among the AC site and species populations explained by the first two axes of the PCA is also presented.

Populations	**Climatic niche overlap (D)**	**Equivalency**	**Similarity** Population → AC site	**Similarity** AC site → Population
Alps	0.246	0.0198	0.07921	0.0099
Pyrenees	0.008	0.0198	0.50495	0.44554
Cantabrians	0	0.0198	0.73267	0.55446
Massif Central	N/A*	N/A*	N/A*	N/A*
Vosges	0.001	0.0198	0.45545	0.32673
Apennines (Central)	0	0.0198	1	1
Dinaric Alps	0.114	0.0198	0.22772	0.11881
AMK	0.179	0.0198	0.29703	0.17822
Pindus Mts. (North)	N/A*	N/A*	N/A*	N/A*
Variation	PC1	60.79%		
	PC2	19.76%		

*Test not applicable due to limited sample size.

Appendix 6 Table A6.14. Climatic niche comparisons between European populations of the Yellow-billed Chough *Pyrrhocorax graculus* and a potential assisted colonisation site in the Upper Eastern Carpathians. The variation among the AC site and species populations explained by the first two axes of the PCA is also presented.

Populations	**Climatic niche overlap (D)**	**Equivalency**	**Similarity** Population → AC site	**Similarity** AC site → Population
Alps	0.023	0.0198	0.18812	0.15842
Pyrenees	0	0.0198	1	1
Cantabrians	0	0.0198	1	1
Apennines	N/A*	N/A*	N/A*	N/A*
Corsican Mts.	0	0.0198	1	1
Montes Vascos	0	0.0198	1	1
Jura Mts.	N/A*	N/A*	N/A*	N/A*
Dinaric Alps	0.001	0.0198	0.41584	0.21782
AMK	0.046	0.0198	0.29703	0.10891
Balkan Mts.	N/A*	N/A*	N/A*	N/A*
BMG	0.311	0.09901	0.0198	0.0099
Pindus Mts. (North)	0.009	0.0198	0.43564	0.25743
Pindus Mts. (South)	N/A*	N/A*	N/A*	N/A*
Peloponnese Mts.	N/A*	N/A*	N/A*	N/A*
Crete	N/A*	N/A*	N/A*	N/A*
Variation	PC1	57.96%		
	PC2	22.99%		

*Test not applicable due to limited sample size.

Appendix 6 Table A6.15. Climatic niche comparisons between European populations of the Yellow-billed Chough *Pyrrhocorax graculus* and a potential assisted colonisation site in the Lower Eastern Carpathians. The variation among the AC site and species populations explained by the first two axes of the PCA is also presented.

Populations	**Climatic niche overlap (D)**	**Equivalency**	**Similarity** Population → AC site	**Similarity** AC site → Population
Alps	0.029	0.0198	0.17822	0.16832
Pyrenees	0	0.0198	0.77228	0.46535
Cantabrians	0	0.0198	0.64356	0.58416
Apennines	N/A*	N/A*	N/A*	N/A*
Corsican Mts.	0	0.0198	1	1
Montes Vascos	0	0.0198	1	1
Jura Mts.	N/A*	N/A*	N/A*	N/A*
Dinaric Alps	0.005	0.0198	0.51485	0.21782
AMK	0.067	0.0198	0.22772	0.09901
Balkan Mts	N/A*	N/A*	N/A*	N/A*
BMG	0.273	0.17822	0.0297	0.0198
Pindus Mts.	0.014	0.0198	0.49505	0.17822
Crete	N/A*	N/A*	N/A*	N/A*
Pindus Mts. (South)	N/A*	N/A*	N/A*	N/A*
Peloponnese Mts.	N/A*	N/A*	N/A*	N/A*
Variation	PC1	57.96%		
	PC2	22.99%		

*Test not applicable due to limited sample size.

Appendix 6 Table A6.16. Climatic niche comparisons between European populations of the Yellow-billed Chough *Pyrrhocorax graculus* and a potential assisted colonisation site in the Grampian Mountains. The variation among the AC site and species populations explained by the first two axes of the PCA is also presented.

Populations	**Climatic niche overlap (D)**	**Equivalency**	**Similarity** Population → AC site	**Similarity** AC site → Population
Alps	0.022	0.0198	0.30693	0.0495
Pyrenees	0.01	0.0198	0.37624	0.07921
Cantabrians	0	0.0198	0.67327	0.34653
Apennines	N/A*	N/A*	N/A*	N/A*
Corsican Mts.	0	0.0198	0.10891	0.0495
Montes Vascos	0	0.0198	0.34653	0.08911
Jura Mts.	N/A*	N/A*	N/A*	N/A*
Dinaric Alps	0.001	0.0198	0.57426	0.23762
AMK	0	0.0198	0.77228	0.48515
Balkan Mts.	N/A*	N/A*	N/A*	N/A*
BMG	0	0.0198	1	1
Pindus Mts. (North)	0.002	0.0198	0.84158	0.22772
Crete	N/A*	N/A*	N/A*	N/A*
Pindus Mts. (South)	N/A*	N/A*	N/A*	N/A*
Peloponnese Mts.	N/A*	N/A*	N/A*	N/A*
Variation	PC1	60.89%		
	PC2	22.33%		

*Test not applicable due to limited sample size.

Appendix 6 Table A6.17. Climatic niche comparisons between European populations of the Yellow-billed Chough *Pyrrhocorax graculus* and a potential assisted colonisation site in the Northern Tatras (Western Carpathians). The variation among the AC site and species populations explained by the first two axes of the PCA is also presented.

Populations	**Climatic niche overlap (D)**	**Equivalency**	**Similarity** Population → AC site	**Similarity** AC site → Population
Alps	0.505	0.0198	0.0099	0.0099
Pyrenees	0.135	0.0198	0.47525	0.09901
Cantabrians	0.002	0.0198	0.92079	0.39604
Apennines	N/A*	N/A*	N/A*	N/A*
Corsican Mts.	0	0.0198	0.90099	0.57426
Montes Vascos	0	0.0198	0.9505	0.56436
Jura Mts.	N/A*	N/A*	N/A*	N/A*
Dinaric Alps	0.068	0.0198	0.51485	0.16832
AMK	0.084	0.0198	0.49505	0.21782
Balkan Mts.	N/A*	N/A*	N/A*	N/A*
BMG	0.019	0.0198	0.13861	0.15842
Pindus Mts. (North)	0.026	0.0198	0.81188	0.21782
Crete	N/A*	N/A*	N/A*	N/A*
Pindus Mts. (South)	N/A*	N/A*	N/A*	N/A*
Peloponnese Mts.	N/A*	N/A*	N/A*	N/A*

Variation	PC1	59.01%
	PC2	22.25%

*Test not applicable due to limited sample size.

Appendix 6 Table A6.18. Climatic niche comparisons between European populations of the Yellow-billed Chough *Pyrrhocorax graculus* and a potential assisted colonisation site in the Low Tatras (Western Carpathians). The variation among the AC site and species populations explained by the first two axes of the PCA is also presented.

Populations	**Climatic niche overlap (D)**	**Equivalency**	**Similarity** Population → AC site	**Similarity** AC site → Population
Alps	0.215	0.0198	0.10891	0.0396
Pyrenees	0.014	0.0198	0.61386	0.32673
Cantabrians	0.001	0.0198	0.80198	0.57426
Apennines	N/A*	N/A*	N/A*	N/A*
Corsican Mts.	0	0.0198	1	1
Montes Vascos	0	0.0198	0.80198	0.66337
Jura Mts.	N/A*	N/A*	N/A*	N/A*
Dinaric Alps	0.109	0.0198	0.40594	0.15842
AMK	0.208	0.0198	0.27723	0.16832
Balkan Mts.	N/A*	N/A*	N/A*	N/A*
BMG	0.085	0.0198	0.18812	0.07921
Pindus Mts. (North)	0.042	0.0198	0.74257	0.23762
Crete	N/A*	N/A*	N/A*	N/A*
Pindus Mts. (South)	N/A*	N/A*	N/A*	N/A*
Peloponnese Mts.	N/A*	N/A*	N/A*	N/A*
Variation	PC1	59.01%		
	PC2	22.25%		

*Test not applicable due to limited sample size.

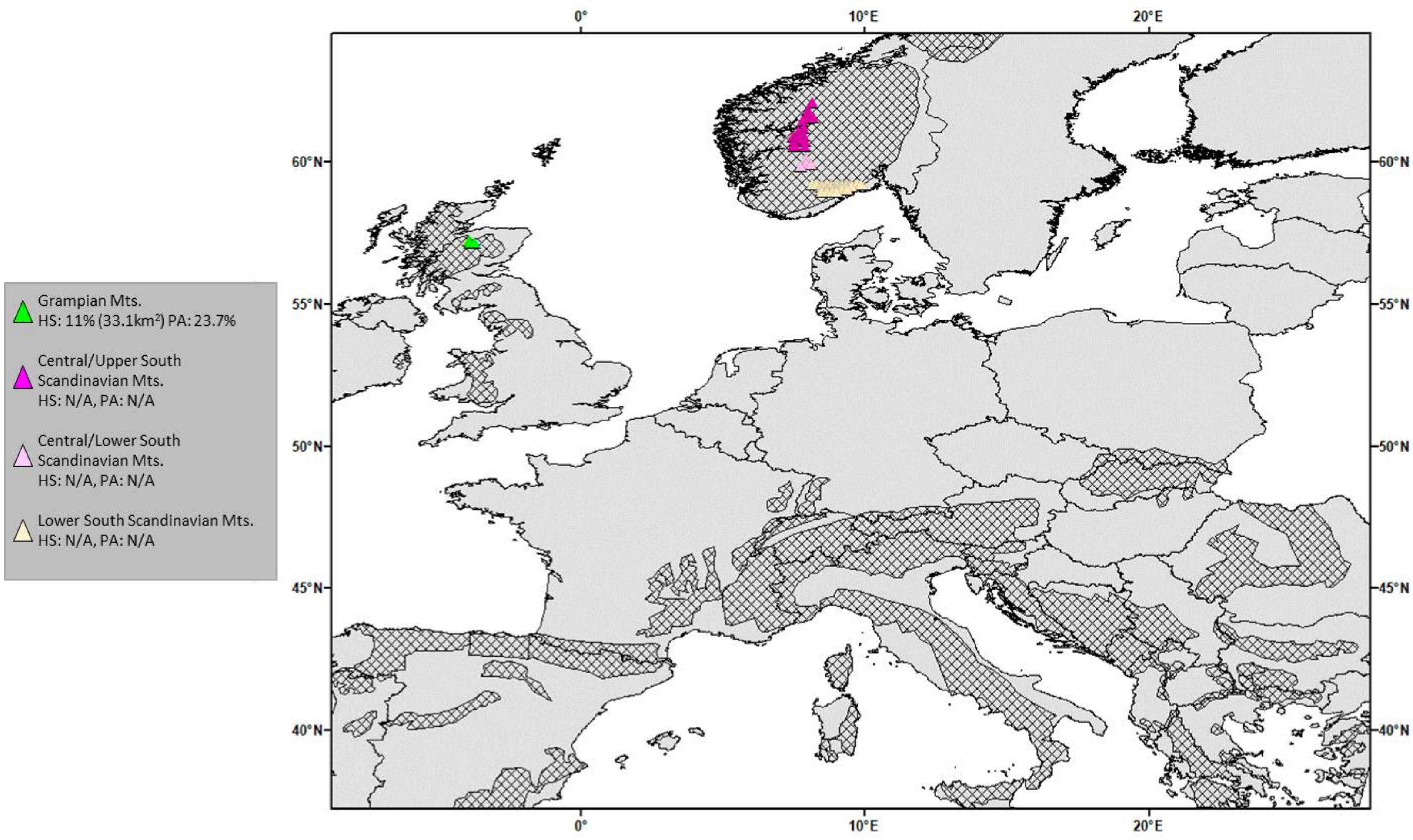
Appendix 6 Table A6.19. Climatic niche comparisons between European populations of the Yellow-billed Chough *Pyrrhocorax graculus* and a potential assisted colonisation site in the Southern Carpathians. The variation among the AC site and species populations explained by the first two axes of the PCA is also presented.

Populations	**Climatic niche overlap (D)**	**Equivalency**	**Similarity** Population → AC site	**Similarity** AC site → Population
Alps	0.035	0.0198	0.08911	0.05941
Pyrenees	0	0.0198	0.62376	0.42574
Cantabrians	0	0.0198	0.63366	0.42574
Apennines	N/A*	N/A*	N/A*	N/A*
Corsican Mts.	0	0.0198	1	1
Montes Vascos	0	0.0198	1	1
Jura Mts.	N/A*	N/A*	N/A*	N/A*
Dinaric Alps	0.008	0.0198	0.26733	0.13861
AMK	0.069	0.0198	0.18812	0.0297
Balkan Mts.	N/A*	N/A*	N/A*	N/A*
BMG	0	0.0198	0.26733	0.19802
Pindus Mts. (North)	0.003	0.0198	0.56436	0.26733
Crete	N/A*	N/A*	N/A*	N/A*
Pindus Mts. (South)	N/A*	N/A*	N/A*	N/A*
Peloponnese Mts.	N/A*	N/A*	N/A*	N/A*

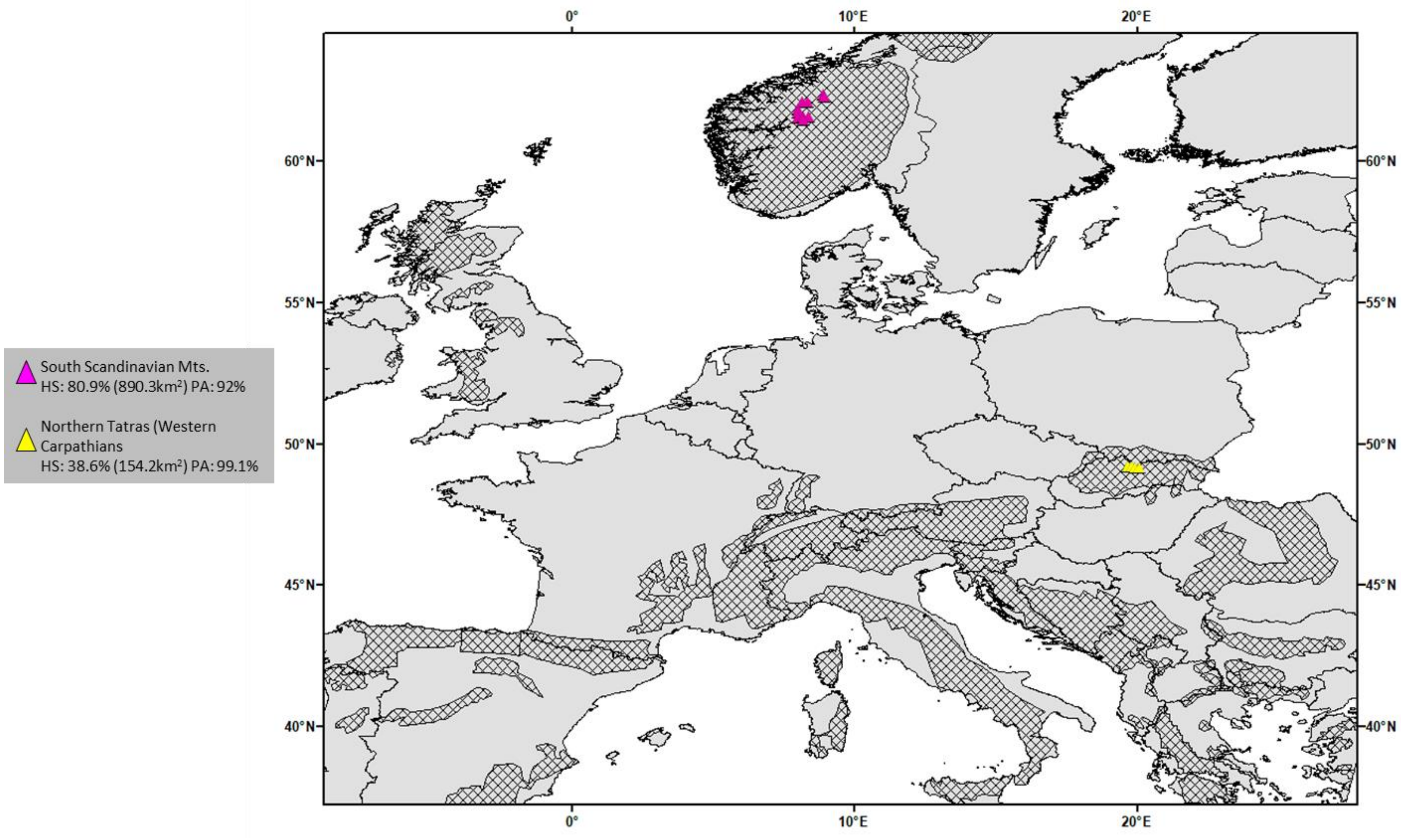
Variation	PC1	57.96%
	PC2	22.99%

*Test not applicable due to limited sample size.

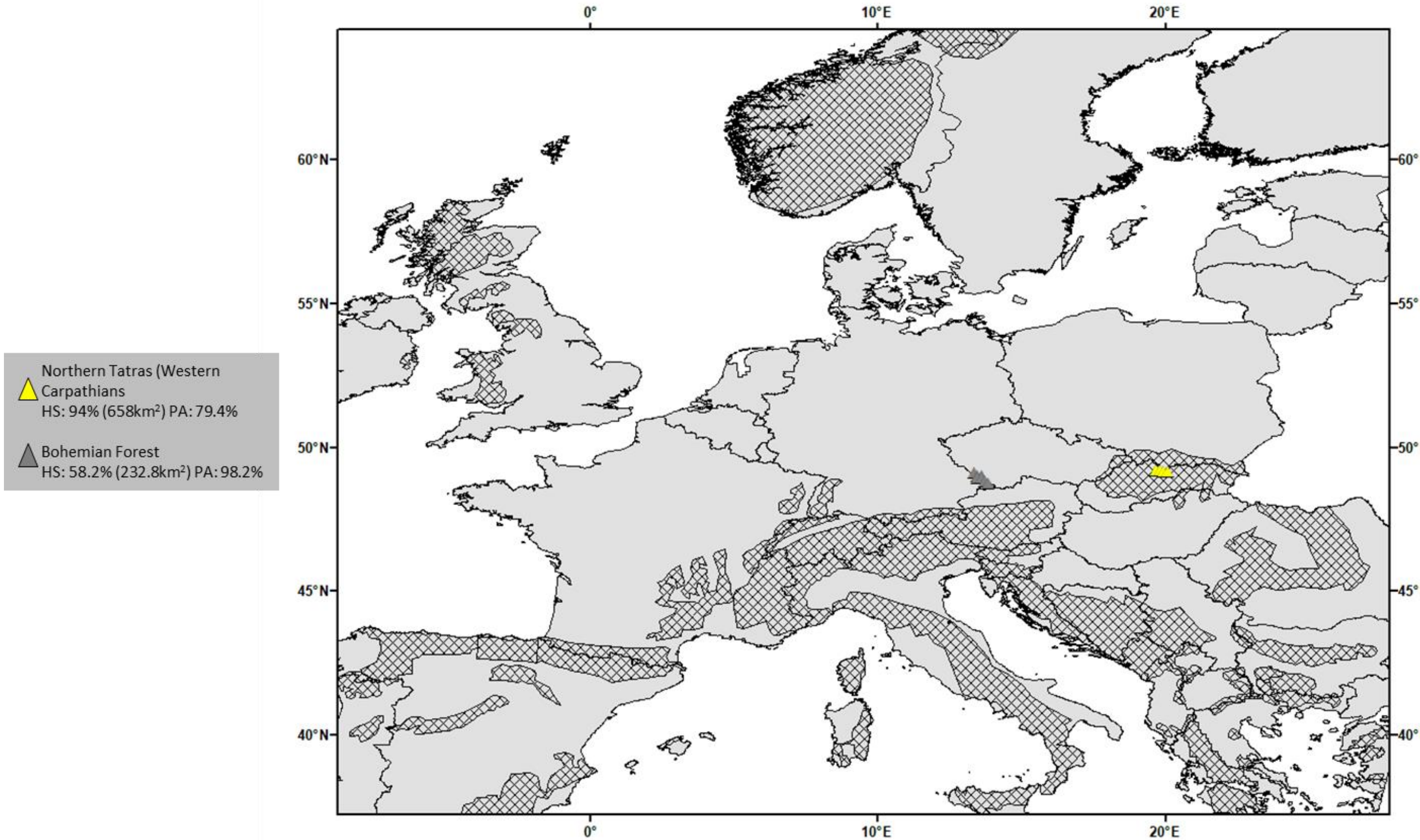
Appendix 7 – Assisted colonisation site maps



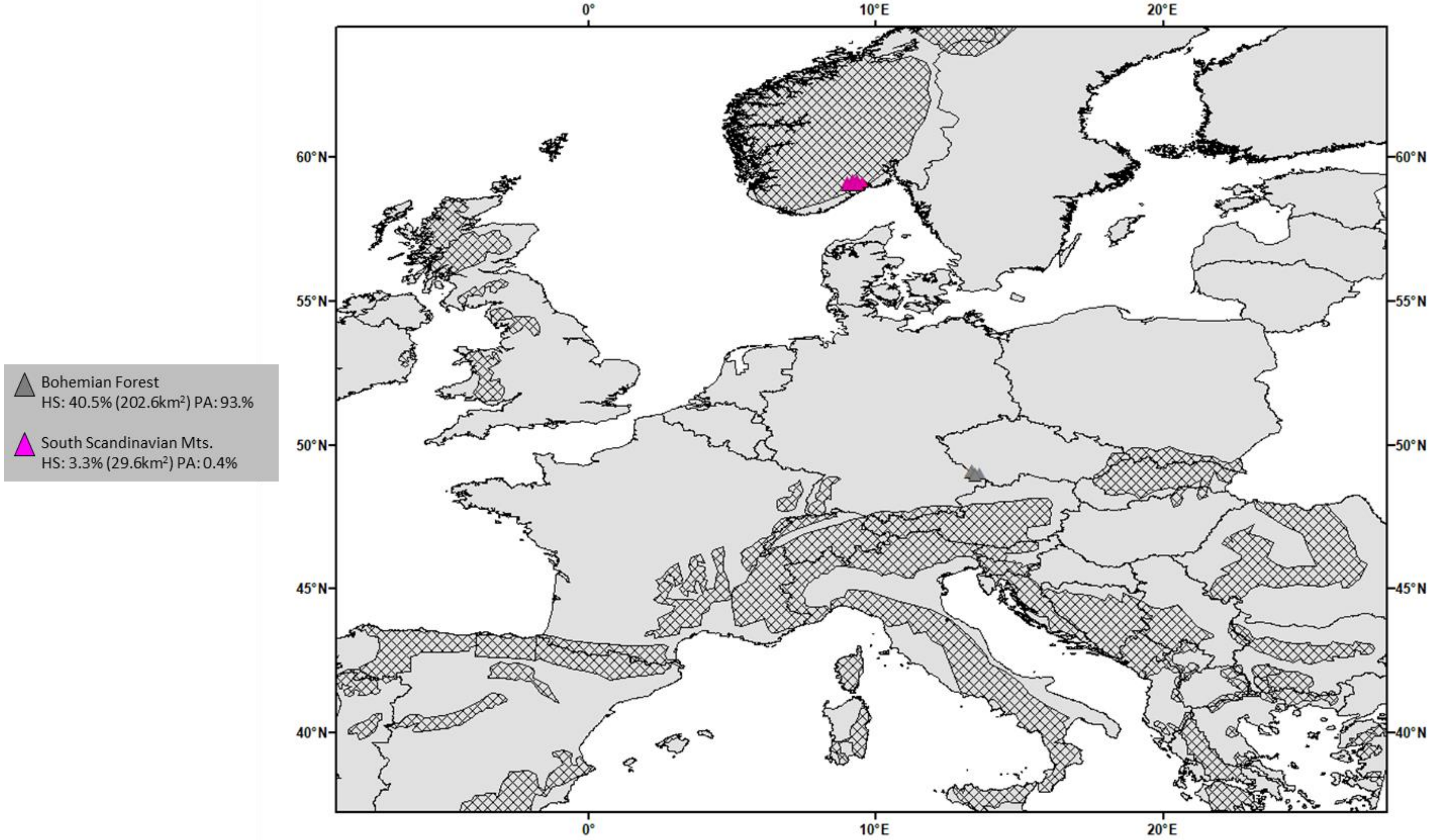
Appendix 7 Fig. A7.1. Potential assisted colonisation sites in Europe for the Alpine Accentor *Prunella collaris*. HS = Habitat suitability, PA = Protected area coverage. HS represents the proportion of the total area of the climatically suitable cells (10 x 10km) containing suitable habitat. PA coverage represents the proportion of suitable habitat at each site that is protected under the Natura 2000 network (or Nationally Designated Areas for sites outside the EU). N/A = Insufficient major habitat.



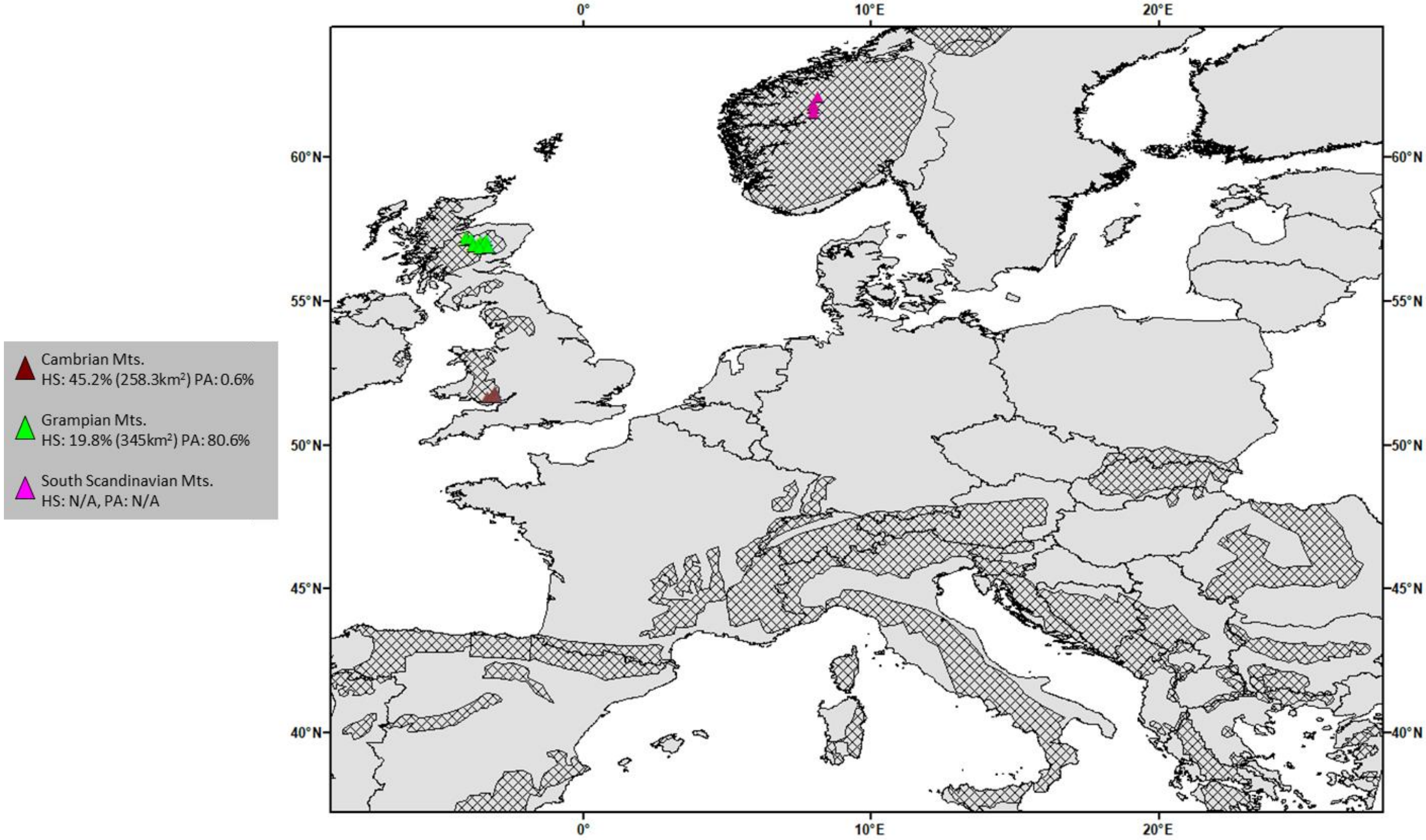
Appendix 7 Fig. A7.2 Potential assisted colonisation sites in Europe for the Bearded Vulture *Gypaetus barbatus*. HS = Habitat suitability, PA = Protected area coverage. HS represents the proportion of the total area of the climatically suitable cells (10 x 10km) containing suitable habitat. PA coverage represents the proportion of suitable habitat at each site that is protected under the Natura 2000 network (or Nationally Designated Areas for sites outside the EU).



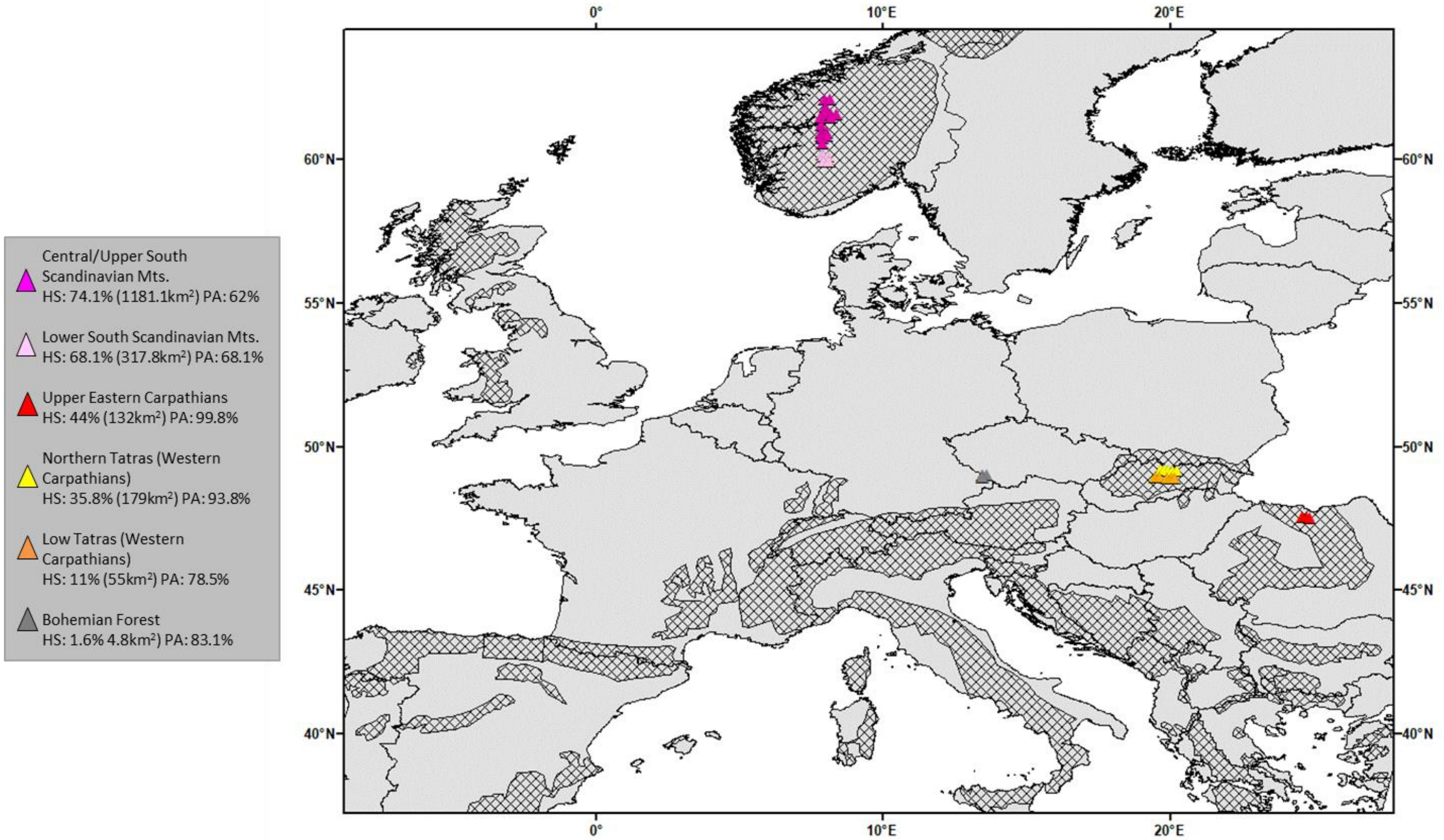
Appendix 7 Fig. A7.3 Potential assisted colonisation sites in Europe for the Citril Finch *Carduelis citrinella*. HS = Habitat suitability, PA = Protected area coverage. HS represents the proportion of the total area of the climatically suitable cells (10 x 10km) containing suitable habitat. PA coverage represents the proportion of suitable habitat at each site that is protected under the Natura 2000 network (or Nationally Designated Areas for sites outside the EU).



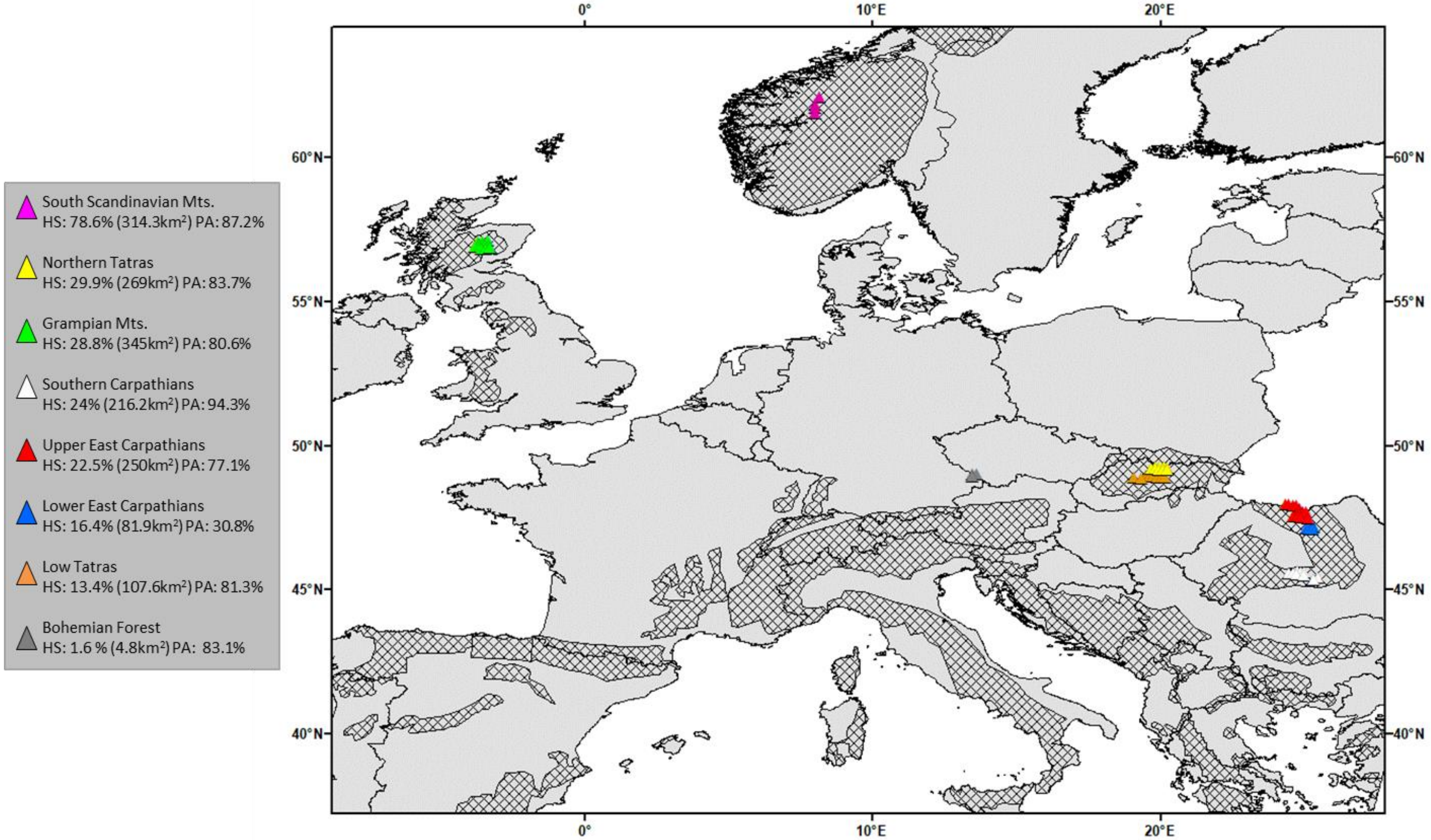
Appendix 7 Fig. A7.4 Potential assisted colonisation sites in Europe for the Rufous-tailed Rock Thrush *Monticola saxatilis*. HS = Habitat suitability, PA = Protected area coverage. HS represents the proportion of the total area of the climatically suitable cells (10 x 10km) containing suitable habitat. PA coverage represents the proportion of suitable habitat at each site that is protected under the Natura 2000 network (or Nationally Designated Areas for sites outside the EU).



Appendix 7 Fig. A7.5 Potential assisted colonisation sites in Europe for the Water Pipit *Anthus spinoletta*. HS = Habitat suitability, PA = Protected area coverage. HS represents the proportion of the total area of the climatically suitable cells (10 x 10km) containing suitable habitat. PA coverage represents the proportion of suitable habitat at each site that is protected under the Natura 2000 network (or Nationally Designated Areas for sites outside the EU). N/A = Insufficient major habitat.



Appendix 7 Fig. A7.6 Potential assisted colonisation sites in Europe for the White-winged Snowfinch *Montifringilla nivalis*. HS = Habitat suitability, PA = Protected area coverage. HS represents the proportion of the total area of the climatically suitable cells (10 x 10km) containing suitable habitat. PA coverage represents the proportion of suitable habitat at each site that is protected under the Natura 2000 network (or Nationally Designated Areas for sites outside the EU).



Appendix 7 Fig. A7.7 Potential assisted colonisation sites in Europe for the Yellow-billed Chough *Pyrrhocorax graculus*. HS = Habitat suitability, PA = Protected area coverage. HS represents the proportion of the total area of the climatically suitable cells (10 x 10km) containing suitable habitat. PA coverage represents the proportion of suitable habitat at each site that is protected under the Natura 2000 network (or Nationally Designated Areas for sites outside the EU).