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### Title

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### Permalink

<https://escholarship.org/uc/item/7h63h4s8>

### Journal

Integrative Zoology, 11(1)

### ISSN

1749-4869

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### Publication Date

2016

### DOI

10.1111/1749-4877.12167

Peer reviewed

## REVIEW

# The integration of climate change, spatial dynamics, and habitat fragmentation: A conceptual overview

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## Abstract

A growing number of studies have looked at how climate change alters the effects of habitat fragmentation and degradation on both single and multiple species; some raise concern that biodiversity loss and its effects will be exacerbated. The published literature on spatial dynamics (such as dispersal and metapopulation dynamics), habitat fragmentation and climate change requires synthesis and a conceptual framework to simplify thinking. We propose a framework that integrates how climate change affects spatial population dynamics and the effects of habitat fragmentation in terms of: (i) habitat quality, quantity and distribution; (ii) habitat connectivity; and (iii) the dynamics of habitat itself. We use the framework to categorize existing autecological studies and investigate how each is affected by anthropogenic climate change. It is clear that a changing climate produces changes in the geographic distribution of climatic conditions, and the amount and quality of habitat. The most thorough published studies show how such changes impact metapopulation persistence, source–sink dynamics, changes in species' geographic range and community composition. Climate-related changes in movement behavior and quantity, quality and distribution of habitat have also produced empirical changes in habitat connectivity for some species. An underexplored area is how habitat dynamics that are driven by climatic processes will affect species that live in dynamic habitats. We end our discussion by suggesting ways to improve current attempts to integrate climate change, spatial population dynamics and habitat fragmentation effects, and suggest distinct areas of study that might provide opportunities for more fully integrative work

**Key words:** global change, global climate change, habitat fragmentation, metapopulation, spatial dynamics.

## INTRODUCTION

Global climate change and the dual effects of habitat loss and fragmentation are two of the most pressing

concerns for biodiversity (Sala *et al.* 2000). Studies rank habitat loss and fragmentation as leading causes of imperilment of species in the USA (Wilcove *et al.* 1998) and as important globally but harder to rank against other factors at such a large scale (Sala *et al.* 2000; Baillie *et al.* 2004). Some authors predict that species losses from global climate change will surpass those from habitat loss (Leadley *et al.* 2010). Predictions from 2050 mid-range global climate change projections range from 15% to 37% species loss (Thomas *et*

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*al.* 2004). Ecologists are faced with the problem of reading a large literature on the ecological effects of habitat fragmentation and related spatial dynamics, and an already vast and fast growing literature on the ecological effects of global climate change. Importantly, there is a need to consider the combined effects of drivers of global habitat change, such as fragmentation and climate change (e.g. Sala *et al.* 2000; Mantyka-Pringle *et al.* 2012). Such combined effects are the greatest areas of uncertainty in studying the ecological effects of climate change. They are potentially relevant to understanding both the persistence of species within their current ranges under changed climatic conditions and shifts in geographic range, which appear common (Parmesan 2006). While an increasing number of studies have addressed this need by looking at how climate change affects spatial dynamics and the effects of habitat fragmentation, the literature is scattered and we lack a conceptual synthesis.

We reviewed studies and concepts relevant to this topic, and derive a conceptual framework that we hypothesize will help others think about spatial dynamics, fragmentation and climate change in an integrated way. The review consisted of a search of relevant terms (fragmentation, spatial dynamics, metapopulation, metacommunity and source–sink population) and then a branching literature survey to find relevant papers, concentrating on autecological approaches that explicitly address the effects of climate change.

What are the main types of spatial dynamics and effects of habitat fragmentation or loss that are relevant? Most abundant in the published literature are investigations into the effects of patch area and isolation, which have strong theoretical roots, including island biogeography (MacArthur & Wilson 1967), metapopulation (e.g. Hanski & Gilpin 1991) and metacommunity theories (Leibold *et al.* 2004). Despite the prevalence of patch occupancy studies, a broad meta-analysis, covering 785 animal species from varied taxonomic groups, found that patch area and isolation jointly accounted for only 25% of variation in patch occupancy (Prugh *et al.* 2008). It is striking that on average 75% of variation in patch occupancy was unexplained. Adding a variety of species and system traits increased the explanatory power but not markedly (Prugh *et al.* 2008; Prugh 2009). A review of studies looking at species richness also found a lack of consistent effects of patch area and isolation (Debinski & Holt 2000). A variety of factors may help explain the

mixed or weak effects. Some studies found that local population size was a better predictor of occupancy rather than patch area and isolation (e.g. Hanski 1998); other studies were more successful at explaining the dynamic process of extinction rather than snapshots of occupancy (e.g. Pellet *et al.* 2010). More detailed considerations of species' dispersal ability may help for some taxa: for instance, including estimates of the dispersal ability improved the predictive ability of the isolation effect on occupancy for amphibians ( $R^2 = 0.45$ ) but only marginally for birds, mammals and invertebrates ( $R^2 \leq 0.06$ ; Prugh *et al.* 2008). Habitat patches may also not be good islands and species may instead use habitat matrices through more of their life cycle (Davies *et al.* 2001; Prugh *et al.* 2008). Habitat-specific demography has been shown to be important in other studies (e.g. Fleishman *et al.* 2002), and is fleshed out by source–sink theory (Pulliam 1988) and mass effects and species sorting paradigms for metacommunities (Leibold *et al.* 2004). The dynamics of habitat itself may control opportunities for colonization and cause local extinctions in some systems, like those with succession or periodic disturbance that creates or resets successional trajectories of habitat patches. Habitat dynamics have been investigated using metapopulation models (e.g. Hastings 2003), and there are some relatively complete empirical examples, such as Sjögren Gulve's (1994) work on pool frogs. Some empirical fragmentation studies also contain effects that do not fit neatly into most spatial dynamics concepts (Sjögren 1991). For instance, fragmentation-induced edge effects may cause changes in area of habitat, quality of habitat and connectivity (e.g. Murcia 1995).

Turning to global climate change, a wide range of ecological effects have been reported and are potentially relevant to spatial dynamics and fragmentation. Effects have been reported at levels of biological organization ranging from the individual (e.g. Hoffman & Todgham 2010) to entire ecosystems (e.g. Hoegh-Guldberg *et al.* 2010). As Bellard *et al.* (2012) point out, it is hard to know how to integrate studies at these different levels to make predictions of change to ecological systems, although others call for doing so (e.g. Woodward *et al.* 2010). Changes in phenology or timing, and latitudinal or altitudinal shifts in geographical range are the most frequently reported effects of climate change (Parmesan & Yohe 2003; Parmesan 2006). Reports of expected and observed changes in habitat distribution and availability (e.g. Prentice *et al.* 2007) also raise questions about the ability of different species to disperse to maintain

suitable environmental and habitat conditions, and whether species are placed under selective pressure and individual fitness is reduced. Such shifts demand a change in distribution of species requiring particular habitats, or lead us to consider assisted migration (translocation; McLachlan *et al.* 2007). Viewed from the perspective of persistence and climate adaptation of individual species, phenology effects may cause loss of individual fitness or may result from mistiming between interacting species. More generally, determining how species interactions will change as a result of climate change is challenging, and while a few conceptual overviews exist (e.g. Gilman *et al.* 2010), at this point in time our knowledge consists mainly of scattered studies. Examples include situations when a consumer misses peak abundance of a food resource, or flowering and pollinator activity are mismatched in time (e.g. Visser & Both 2005).

The major physical changes in global climate that we view as most relevant to ecological systems are summarized in Table 1. The most obvious changes are shifts in the geographical distribution of climate envelopes (zones with a given set of conditions), with latitudinal and altitudinal shifts in temperatures, albeit with substantial regional variation (e.g. Burrows *et al.* 2011). By contrast, changes in precipitation are more idiosyncratic and likely have more local geographical variation (Diffenbaugh *et al.* 2005). Seasonal changes are also substantial. As Bradshaw and Holzapfel (2006) point out, the greatest changes in mean temperature occur in spring and autumn and in temperate or Arctic conditions, whereas changes in average summer or winter temperature are typically smaller in magnitude (Hartmann *et al.* 2013). Warmer winter temperatures also impact the amount of precipitation falling as rain versus snow (Hartmann *et al.* 2013), which can impact

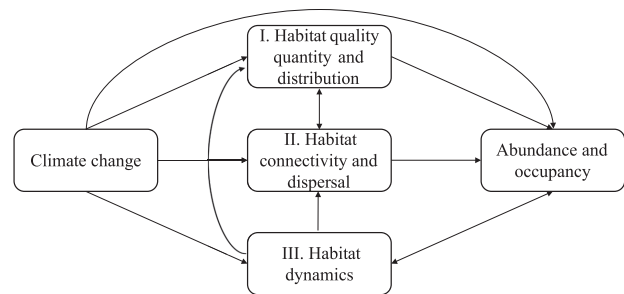
**Table 1** Examples of some major changes in climatic factors and distribution of climatic conditions due to anthropogenic climate change. For spatial “scale” we define “global” as being relatively consistent based on measured records, “regional” as representing a major region such as Central Europe or North America and “local” as being at smaller scales such as a European country or western US state

Climatic variable	Typical change	Scale	Reference
Average temperature over land	Increase	Global	Hartmann <i>et al.</i> (2013)
Sea temperature	Increase but less than over land	Global	Hartmann <i>et al.</i> (2013)
Geographical shift in temperature conditions over land	To poles or increasing elevation	Regional	Burrows <i>et al.</i> (2011)
Geographical shifts in temperature over oceans	To poles, but smaller shifts than over land	Regional	Burrows <i>et al.</i> (2011)
Season length	Increase in temperate regions	Regional	Bradshaw and Holzapfel (2006)
Changed precipitation	Increase in Northern Hemisphere, variable elsewhere	Local	Hartmann <i>et al.</i> (2013)
Frequency of extreme hot days or periods	Increase over North America and Europe	Regional–global	Hartmann <i>et al.</i> (2013)
Frequency of extreme cold days or periods	Decrease over North America and Europe	Regional–global	Hartmann <i>et al.</i> (2013)
Number of extreme high rainfall events	Increase in North America and Europe	Local	Hartmann <i>et al.</i> (2013)
Drought frequency and duration	Increase in Mediterranean and West Africa, decrease in North America and north-west Australia	Regional	Hartmann <i>et al.</i> (2013)
Amount of snow	Less snow and more rain in Western North America, less snow and precipitation in Japan	Local to regional	Hartmann <i>et al.</i> (2013)

water storage in snow packs and glaciers. Variation in climate is also expected to increase, which in terms of temperatures means more extreme hot summer temperatures, and these have been observed with a high confidence (Hartmann *et al.* 2013). More hot weather may exasperate the effects of limited water availability in some regions. Conversely, the number of extreme cold days in winter have declined (with a high degree of confidence, Hartmann *et al.* 2013; Peterson *et al.* 2013). We have limited to medium confidence that extreme events such as floods and droughts have increased in area and duration, and low confidence that hurricanes and tornadoes have increased (Hartmann *et al.* 2013). Floods and droughts also show substantial geographical variation (Peterson *et al.* 2013). Predictions of extreme events are increasingly more uncertain at regional compared to global scales, because data for these events are limited (Hartmann *et al.* 2013). Drought and subsequent tree mortality (e.g. Allen *et al.* 2010), and increased spring and summer temperatures and earlier spring snowmelt may increase the frequency and extent of wildfire (Westerling *et al.* 2006). Finally, there have been substantial land versus sea differences in temperature change since 1960. Rates of warming over land have been greater than those over oceans and larger gradients in temperature change (per km) exist over land than oceans (Burrows *et al.* 2011). Consequently, a species would need to move further over land than through or over the oceans to maintain similar temperature conditions.

We pose the following three questions about how climate change alters spatial dynamics and the effects of habitat loss and fragmentation. First, how does climate change alter habitat quantity, quality and distribution? Second, how does climate change alter the connectivity and dispersal of species across a landscape? Third, how might habitat dynamics be modified by climate change? After addressing these three questions we summarize some relevant areas of research that are in the early stages of development and are in need of further work.

Figure 1 presents a conceptual diagram for how we relate these habitat factors to climate and metapopulation dynamics, which we hypothesize will be a useful way of thinking about climate change, spatial dynamics and fragmentation for other systems. The diagram emphasizes that the effects of quantity, quality and distribution of habitat are not independent of habitat connectivity (and dispersal), and that habitat dynamics also affect habitat connectivity. For instance, changes in the distribution of habitat are likely to also impact dispersal.



**Figure 1** Conceptual diagram for how climate change affects metapopulation dynamics. The diagram includes direct effects of climate on population abundance and habitat patch occupancy as well as indirect effects through the quality/quantity of habitat, connectivity of habitat and dynamics of habitat (e.g. succession). Arrows between abundance/occupancy and habitat dynamics or quality/quantity could also be 2-way arrows because there may be feedbacks from consumers in patches and habitat state. Individual effects, such as physiological changes, are not included in the diagram.

## CLIMATE CHANGE AND THE QUANTITY, QUALITY AND DISTRIBUTION OF HABITAT

### Five categories of effects of habitat change

Changes in the quantity, quality and distribution of habitat have a wide range of effects on spatial dynamics, the most obvious of which are summarized in Table 2 (effects 1–5). Considering them in five separate categories helps to simplify thinking.

Most directly, the quality and quantity of habitat in a given location may change (Table 2, effect 1), with habitat areas either being lost or gained entirely, or the quality of existing areas shifting. Species may adapt, acclimate or disperse in response to change, or decline in abundance or become locally extinct. Adaptation or acclimation may be through mechanisms that do not involve spatial dynamics. The extent of adaptation or acclimation is also expected to depend on the degree of habitat specialism, because habitat generalists may be more buffered against change through having multiple habitat types they can use. Hence, it is a somewhat common prediction that habitat specialists are more vulnerable to climate change (e.g. Morrongiello *et al.* 2011) or cannot shift their geographical range to remain in similar temperature conditions (e.g. Thomas 2010).

**Table 2** Summary of some of the major effects of climate change on spatial dynamics and the effects of habitat fragmentation.

Effect	Responses	Examples
<b>I. Effects through habitat quantity, quality and distribution</b>		
1. Change in quality or quantity	Adapt, acclimate, disperse or change in abundance and/or distribution; small population size effects may decline or be exacerbated (Allee effects, inbreeding etc.); sources may become sinks and vice versa	Travis (2003); Carroll (2007).
2. Changes in the latitudinal and altitudinal distribution of habitat	Latitudinal or altitudinal migrants may need to move further to reach suitable conditions	Møller <i>et al.</i> (2006)
3. Refugia important	Heterogeneous landscapes will maintain species diversity better; source–sink dynamics and metapopulation dynamics more likely	Seavy <i>et al.</i> (2009); Morrongiello <i>et al.</i> (2011)
4. Time lag between climate change and habitat change	Reduced fitness (sink conditions), abundance, geographic range	Anderson <i>et al.</i> (2009); Bertrand <i>et al.</i> (2011)
5. Loss or gain of source populations because of altered habitat	Large declines in regional distributions may occur if rescue effects or colonization lost, or increases if source populations gained	Davies <i>et al.</i> (1998); Thomas <i>et al.</i> (2001); Warren <i>et al.</i> (2001); Fordham <i>et al.</i> (2013)
<b>II. Effects through habitat connectivity and dispersal</b>		
6. Changes in habitat connectivity	Structural connectivity changes may result from changes in the quality and quantity of habitat	Example studies Manning <i>et al.</i> 2009; Breed <i>et al.</i> 2011
7. Need to disperse to maintain climate envelope	Need to disperse to areas with suitable climate conditions; geographical distribution of suitable areas matters; ability to cross non-habitat areas important; distances between different habitat areas influence the potential for source–sink dynamics; translocation needed for some species	Schweiger <i>et al.</i> (2008); Bertrand <i>et al.</i> (2011)
8. Altered habitat-dependent dispersal	Emigration altered by habitat conditions	Altermatt <i>et al.</i> (2008)
9. Altered habitat preference/use	Settlement or habitat selection may change immigration patterns if patch quality changes	Wilbert <i>et al.</i> (2000)
10. Altered feedback through population dynamics	Changes in reproduction or survival in response to climate may alter how much density-dependent dispersal occurs	Parn <i>et al.</i> (2012)
11. Climate change alters organismal movement directly	Warmer temperatures may reduce development times and thereby shorten the dispersal time in marine planktonic larvae; warmer temperatures may increase activity periods of poikilotherms; altered bird migration during warmer periods or with certain wind directions	Battisti <i>et al.</i> (2006); Møller <i>et al.</i> (2006); O'Connor <i>et al.</i> (2007); Cormont <i>et al.</i> (2011)
<b>III. Effects through habitat dynamics</b>		
12. Altered frequency of habitat dynamics	An altered frequency of fire or flood (etc.) may change the amount of habitat patches for a target species and spatiotemporal dynamics	Lawson <i>et al.</i> (2010)
13. Altered spatial scale of habitat dynamics	Droughts and fires may change in spatial extent with climate change altering the amount of habitat and distances between patches (and dispersal)	Jones <i>et al.</i> (2014)

Species' acclimatization or adaptation to climate change is exacerbated by the fact that most species have small geographic ranges, and, furthermore, rare species tend to have low abundance within their range, making them vulnerable to extinction (Manne & Pimm 2001; Pimm 2008). The combined negative effects of small geographic range, specificity and limited dispersal on persistence are illustrated in lattice model simulations by Travis (2003).

Habitats are expected to shift to higher latitudes and altitudes, which may, in turn, affect movement and population dynamics (Table 2, effect 2). For instance, Bertrand *et al.* (2011) looked at expected shifts in plant community composition (reflecting habitat) in France, comparing predictions from climate envelopes to observed changes in species composition, and found that on average species had responded to only a fraction of observed warming over a 44-year period. Furthermore, highland community composition changed to account for 0.57 °C mean requirements of 1.07 °C observed temperature change, whereas lowland species accounted for only 0.02 °C of 1.11 °C observed temperature change. In both cases it is clear that the less than complete change in community composition to match temperature shifts mean that some community members will be in suboptimal conditions and would experience selection pressure for change through lowered fitness (Bertrand *et al.* 2011). Such changes may produce an increase in sink population status, as indicated by a finite growth rate,  $\lambda < 1$ . Another example helps illustrate the need for population dispersal or translocation with changing habitat distributions. For a European butterfly, Schweiger *et al.* (2008) predicted that climate change will cause a decrease in the spatial overlap in geographic ranges with its host plant and that some of the future suitable habitat areas for the plant are so distant that the probability (or rate) of colonization by the butterfly is expected to be low. Such spatial mismatches, either between a species and its future habitat, or between interacting species' may be far more common than we currently realize, and add to changes in the quantity of habitat available to a species or the need for dispersal.

Habitat heterogeneity and the kinds of habitat available may also change under climate change. Refuge habitats (Table 2, effect 3) may become particularly important (e.g. Morrongiello *et al.* 2011). Areas with topographic relief are likely to contain a greater diversity of habitats relative to equivalent lowland areas (e.g. Bertrand *et al.* 2011). Bertrand *et*

*al.* (2011) found that the distances required to move to maintain constant average temperature conditions were greater in lowland areas than highland areas because of this greater heterogeneity in the latter. Bertrand *et al.* (2011) also found connectivity of these habitats to be important: lowland habitats were more fragmented than upland habitats, which might impede dispersal between lowland habitat areas. In another example, Seavy *et al.* (2009) suggested that riparian areas in lowlands increase spatial habitat heterogeneity and are expected to provide connected refugia in changing climates. The same is likely to apply to depth of water bodies as it does to elevation on land. Of course, moving up mountains (or deeper in oceans) has its limits. High elevation European plant species are expected to decline in area as they are forced off of the top of mountains, but only in areas that are expected to experience more intense warming and under certain climate scenarios (Engler *et al.* 2011).

Of further relevance will be whether habitat suitability and quantity is determined by proximate factors such as temperature, or whether a longer-term biotic change (such as in vegetation) is required for suitability. Longer-term changes may create a time lag before previously unsuitable habitat areas become suitable (Table 2, effect 4). Frequently metapopulation models assume that there would be habitat conversion caused by climate change and that this would be sufficiently rapid to make new habitat available by the time current habitat has become unsuitable. For instance, Anderson *et al.* (2009) predicted future occupancy and abundance scenarios for metapopulations of the volcano rabbit [*Romerolagus diazi* (Ferrai-Pérez, 1893)] and point out that the species is not constrained elevationally but is constrained by the type of vegetation present. Such time lags for habitat change and their effects on habitat availability merit further study for species of concern.

We know from theory and empirical study of source-sink systems (and mass effects) that species may be present even in habitat where they could not sustain populations in the long term. In such scenarios the loss of source populations could trigger substantial changes in the distribution of a species (Table 2, effect 5). As Davies *et al.* (1998) illustrate with *Drosophila* species in incubators, habitat quality may depend on temperature and species may be maintained in sink populations (and habitats) where temperature conditions do not permit long-term persistence if dispersal from source populations is sufficient. Similarly, a modeling study of two Australian abalone species showed that although

winter climate warming predicted an increase in source habitat, when demography was included the species actually declined in habitat area occupied because of negative effects of summer temperature increases and subsequent loss of rescue (dispersal) effects (Fordham *et al.* 2013). Consequently, the distance and juxtaposition of source and sink habitats are relevant to whether or not sink habitats receive immigrants and how many they receive. Therefore, it is relevant to study whether the spatial pattern of source and sink habitats varies because of climatic factors. Of course, we should also recognize that evolution may change the source versus sink status of habitat (e.g. Dias 1996), and, therefore, the longer-term consequences of climate change on such systems should be studied.

### **Interaction among global change drivers?**

Given that habitat loss and land conversion are the prime drivers of biodiversity loss it is important to ask whether climate exacerbates this effect (Opdam & Wascher 2004; de Chazal & Rounsevell 2009). Theoretically, we might find that climate change and habitat change have independent effects (the sum); they may exacerbate one another (more than the sum) or ameliorate one another (less than the sum) (de Chazal & Rounsevell 2009). One common form of exacerbation may be that small populations are vulnerable to loss, inbreeding and Allee effects (Table 2, effect 1); thus, additional loss of fitness from climate change may have a disproportionately large effect (Opdam & Wachter 2004; de Chazal & Rounsevell 2009). There are several examples of this kind of effect. A rapid decrease in green salamander [*Aneides aeneus* (Cope and Packard, 1881)] relative abundance in populations in the USA has been attributed to a synergism of high habitat fragmentation and increased variation in January temperatures since 1970 (Corser 2001). Similar effects of temperature and fragmentation were found for the bay checkerspot butterfly [*Euphydryas editha bayensis* (Sternitzky, 1937)] in the USA (McLaughlin *et al.* 2002), the tiger moth *Artica caja* L., 1758 in Britain (Conrad *et al.* 2002) and Mediterranean butterflies (Stefanescu *et al.* 2004). For land birds, species loss was projected to be most likely for tropical species with small geographic ranges where land-use change was intense (Jetz *et al.* 2007). A meta-analysis based on 168 papers (Mantyka-Pringle *et al.* 2012) found that the best-fitting models predicting species abundance and richness included temperature and precipitation variables and no interactive effects with habitat loss, but model-averaging revealed more

negative effects of habitat loss when temperatures were greater and less when rainfall was greater. The study included 57% birds, 22% arthropods, 9% mammals, 7% plants, 3% reptiles and 2% amphibians, and its generality suggests that further investigation of such effects is merited. Conversely, there are fewer studies that report amelioration of negative habitat loss effects due to climate (although the strictest results of Mantyka-Pringle *et al.* (2012) could also be included in this category). Amelioration of negative habitat loss effects is reported because of increases in available habitat for the comma butterfly (*Hesperia comma* L., 1758) in the UK due to increased temperature in northern areas that were previously unoccupied (Thomas *et al.* 2001). Some other butterfly species in the UK show similar effects (Warren *et al.* 2001).

Studies have used a variety of population models to explore interactions between global-change drivers through evaluating changes in the source–sink status of populations under climate change. Carroll (2007) used a spatially explicit population model to evaluate the source versus sink status of different habitat areas and predicted future distribution for marten [*Martes americana* (Turton, 1886)] and lynx (*Lynx canadensis* Kerr, 1795) in southeastern Canada and northeastern USA under climate change, habitat loss and trapping pressure. The approach identified where each global change driver could produce changes from source to sink status of different habitat areas in areas subject to habitat fragmentation. Overall, reductions in winter snow cover produced the greatest range contractions, but disproportionately large losses of distribution were produced by the interactions between climate change and habitat loss through logging for martens and between climate change and trapping for lynx. Consideration of a variety of global change scenarios helped to show the sensitivity of predictions to model assumptions and to illustrate the utility of such approaches for evaluating changes in metapopulation dynamics with climate change. As with various modeling studies there is a need for such studies to more clearly show the contribution of different global change factors to population dynamics (e.g. source vs sink status).

### **Physical interactions between habitat and microclimate**

More physical interactions between microclimate and habitat change have been proposed. Laurance and Williamson (2001) report an increase in the desiccating effects of drought in fragmented parts



of Amazonia, especially at forest edges, which has caused tree mortality and has, thereby, led to greater habitat loss. Cochrane and Laurance (2009) report that deforestation in the Amazon is reducing moisture in the atmosphere through -evapotranspiration and smoke plumes, which lead to loss of moisture directly, and all of this is associated with an increase in the frequency of forest fires, which exasperates forest loss. Some of the effect of forest edges may be similar in these two studies, with forest edges frequently being next to pastures that are burned to maintain them as pasture, and both loss of moisture and drought exasperating the effect of fires. Damschen *et al.* (2008) point out that wind characteristics are often changed by habitat fragmentation, which alters vegetation structure. This may have various consequences for processes such as wind damage to vegetation, wind-vectored dispersal, and physiological stress through greater evaporation and evapotranspiration (e.g. McConkey *et al.* 2012).

## CLIMATE CHANGE AND DISPERSAL

### Habitat-dependent versus habitat-independent changes in dispersal

A wide range of factors are expected to change organismal movement across landscapes and seasonal migration, which may alter population dynamics, including spatial dynamics (Table 2). A first category of effects of climate change includes habitat-dependent mechanisms (Table 2, effects 6–9), such as habitat loss and fragmentation (Wilcove *et al.* 2000), increasing connectivity through human activities (biotic homogenization [McKinney & Lockwood 1999]), construction of barriers to movement of some organisms, and habitats shifting geographically and in scale because of climate change (Parmesan & Yohe 2003). A second category of effects arises because of changed population densities acting on density-dependent movement (Table 2, effect 10). Finally, organismal movement may be directly affected by climatic factors, such as ambient temperatures or wind speed and direction (Table 2, effect 11). We discuss each of these effects in detail.

At a landscape scale, changes in the amount of habitat -and its spatial distribution may alter the ability of species to move across a landscape (Table 2, effect 6). Such an effect is depicted in graph-theoretic approaches to connectivity that combine spatially explicit habitat data with the ability of a species to disperse a given

distance (reviewed by Calabrese & Fagan 2004). Such approaches include a scale-dependency that comes from a species ability to cross gaps, and, hence, structural connectivity has to be combined with species characteristics to some extent to become actual organismal dispersal. The generalizability of structural approaches may be questioned. For instance, Angert *et al.* (2011) show that species traits are poor predictors of range expansion for several major taxonomic groups, and suggest investigations of habitat fragmentation and availability along with relevant natural history variation among large numbers of species. However, it is worth recognizing that there may be changes in both habitat itself and organismal movement, which some empirical examples illustrate. Some studies suggest that when habitat fragmentation leaves scattered patches of habitat, such as scattered trees, this may facilitate dispersal across a landscape, which may assist both fauna and the trees themselves to stay within a climate envelope (Manning *et al.* 2009; Breed *et al.* 2011). An example helps to illustrate the dispersal effect: several species of woodland birds in the UK showed greater spatial synchrony of populations when a larger amount of woodland remained in the landscape (Bellamy *et al.* 2003). Similarly, Bertrand *et al.* (2011) found a lower degree of habitat fragmentation in highland areas than lowland areas and suggested that greater habitat connectivity contributed to more plant community composition changes over a 44-year period in the highlands than in lowlands where large habitat patches were less frequent and distances between patches larger. Hence, climate change altered the effect of structural connectivity differently in highland and lowland areas.

It should be expected that changes in habitat suitability due to climate change will occur unevenly across space, and this may create the need or potential for dispersal (Table 2, effect 7). A variety of examples exist. Arctic terns (*Sterna paradisica* Pontoppidan, 1763) have increased natal dispersal distance progressively since the 1930s, which coincided with temporal trends in the North Atlantic Oscillation index (Møller *et al.* 2006). While long-term trends in distance could be related to distances required to reach given climatic conditions, year-to-year variation showed more complex patterns and later arriving breeding birds had lower reproductive success (Møller *et al.* 2006).

Some species may alter emigration in response to changing habitat conditions (Table 2, effect 8). General modeling work by Regaida *et al.* (2015) shows that production of propagules prior to patch destruction can

strongly enhance metapopulation persistence relative to more continuous production of dispersive propagules through time. In an empirical study Altermatt *et al.* (2008) found changes in the colonization of pools by three species of *Daphnia* in relation to climate. A system of 530 rock pools and three species of *Daphnia* have been extensively studied by Pajunen and Pajunen (2007) since 1982 (Ebert *et al.* 2001; Altermatt *et al.* 2007, 2008, 2009). The system persists as a metapopulation, and small pools desiccate and produce large numbers of dispersing propagules (Altermatt & Ebert 2010). Hence, the system represents an interesting and perhaps somewhat general form of habitat dynamic-dependent dispersal where climate may modify the frequency with which pools receive water (precipitation) and dry out (temperature, wind and humidity).

The last major direct effect of habitat change is likely to operate through habitat preference or use, and likely imply changes in spatial distribution and dynamics (Table 2, effect 9). Habitat selection or habitat use may change depending on weather conditions. For instance, Wilbert *et al.* (2000) describe changing nest locations of martens (*M. americana*), with increased use of subnival (under-snow) locations in cold winters and above-snow locations in warmer winters.

Feedbacks between dispersal and population dynamics may arise if dispersal is density dependent (Table 2, effect 10). An effect of weather on population size, which altered emigration, was seen in populations of house sparrows (*Passer domesticus* L., 1758) in Northern Norway. Warmer temperatures led to greater dispersal from islands without farms that provide year-round food, but not from islands with farms (Pärn *et al.* 2012). The authors suggest that warmer temperatures led to higher population numbers and this may have led to more frequent density-dependent dispersal. While this dispersal is through emigration, more generally, density dependence could also arise during immigration or settlement. Both habitat selection behaviors (Morris 2003; Hanski *et al.* 2011; including optimal foraging: Russell *et al.* 2003; Skorka *et al.* 2009) and density dependence (e.g. Silva *et al.* 2001; Hovestadt & Peothke 2006; Best *et al.* 2007) have been shown to strongly affect metapopulation dynamics.

Direct effects of altered climatic conditions on movement (Table 2, effect 11) may occur either through altered development or behavior, or through more general changes in the activity of poikilothermic organisms that translate into altered dispersal. While some organisms (e.g. migrating birds) may select

when to migrate depending on ambient environmental conditions, poikilothermic (and other) organisms might alter the temperatures experienced by selecting microhabitats in some cases. O'Connor *et al.* (2007) show that there is a relatively uniform scaling of temperature and development time for pelagic marine larvae, which is expected to cause a shortening of average dispersal distance with warming. This assumes that evolution is absent. A net effect is that dispersal and gene flow would be reduced (O'Connor *et al.* 2007). This accords with other studies that show that temperature increases shorten average dispersal distances and reduce the frequency of rare long distance dispersal events for benthic marine organisms with bipartite life cycles (Kinlan *et al.* 2005). For coral reef fish, predictions are more variable, with small temperature increases expected to increase larval survival but larger temperature increases reducing survival and reproduction (Munday *et al.* 2009). Poikilothermic species may increase in activity with increased temperatures and this may lead to greater distances of movement. For instance, for four species of European butterfly, Cormont *et al.* (2011) observed greater activity in warmer and less cloudy conditions and greater net displacement with warmer temperatures. The authors hypothesized that this would reduce the negative effects of habitat fragmentation. It seems likely that other taxa that are limited by low temperatures may show similar effects. At shorter timescales, common buzzard (*Buteo buteo* L., 1758) dispersal distance in the UK was related to warmer weather during the flight period and when winds came from certain directions (Walls *et al.* 2005). These varied examples illustrate that mechanisms involving weather effects during dispersal (and development) merit further study.

### How much dispersal is needed?

A question that frequently arises in the literature is how much dispersal is sufficient to keep pace with climate change. Expansion from a range edge may mean that there are fewer populations that can provide immigrants compared to recolonization within an existing metapopulation. For 289 species of Swiss alpine plants Engler *et al.* (2009) calculated that realistic dispersal rates produced results that were quite close to those for unlimited dispersal, and, hence, dispersal rates were generally sufficient to keep pace with projected climate change. However, as Bertrand *et al.* (2011) found, the required distances needed to be moved by highland plants were shorter than those for

lowland plants (a 1.1-km average shift was required to stay at the same average temperature in highland areas compared to 35.6 km in lowland areas over the 44-year study period). As predicted, highland plant communities did show more change in composition during the study period. A similar result from the UK showed that three butterfly species adequately tracked temperature change during a 19-year warming period by shifting their ranges both northward and elevationally (Franco *et al.* 2006). This was not the case for sedentary and specialist butterfly species in the UK, however, which were found unlikely to gain in distribution due to climatic warming (Warren *et al.* 2001). A more general meta-analysis (Chen *et al.* 2011) showed that there was substantial variation in whether species managed to track climate changes in latitude or elevation, with the greatest shifts being seen in regions with the most warming, and seemingly arbitrary variation across taxa. For instance, birds showed more than the expected latitudinal movement but less altitudinal movement than needed to keep pace with temperature change (Chen *et al.* 2011). An analysis of European trees found more rapid (and sufficient) movements for early successional species but that mid and late successional species lagged behind (Meier *et al.* 2012). Interspecific competition and habitat fragmentation reduced movement rates more than adverse climatic effects (Meier *et al.* 2012).

Details of how climate affects the habitat being dispersed through may also determine the amount of dispersal needed. As a more general example, changes between land and oceanic temperatures are generally parallel, as noted in the Introduction, but larger range shifts are required to maintain constant conditions over land than over oceans (Burrows *et al.* 2011). More specifically, Bennie *et al.* (2013) were better able to predict range expansions of a UK butterfly species when they included details of microclimatic warming of habitat patches; warmer patches were more likely to be occupied during the range expansion. In coral systems, small increases in ocean temperatures are likely to increase coral mortality, which would decrease structural connectivity (Munday *et al.* 2009). Hence, the pace and strength of gradients in changes in physical conditions as well as spatial patterns of pre-existing and changed habitat have direct implications for structural connectivity.

### Dispersal and evolution

It is important to recognize that dispersal, and more generally movement, is under selection. Often

movement is treated as a random or neutral process in spatial population models (Morales *et al.* 2010; Lowe & McPeck 2014), whereas movement ecology incorporates dispersal capacity and behavior, including interactions with dispersal vectors that are both biological and physical (reviewed by Holyoak *et al.* 2008; Nathan *et al.* 2008). Additionally, some forms of movement exert strong effects on regional persistence by creating important nonlinearities and feedbacks between patch occupancy and regional persistence (e.g. Clobert *et al.* 2009). There is a need to simplify the diverse and unwieldy set of factors controlling individual movement (Morales *et al.* 2010), to test their effects in empirical metapopulations, and how they are modified by climate change and evolution in response to it.

## CHANGES IN HABITAT DYNAMICS

Simple metapopulation models demonstrate that habitat dynamics in the form of variation in the average lifetime of patches strongly influence metapopulation persistence (Hastings 2003). The effect of colonization on metapopulation dynamics is dependent on whether habitat dynamics are present (Hodgson *et al.* 2009). So the question is, how might climate change alter habitat dynamics? We can envision changes where the frequency of renewal (destruction and creation) of habitat patches is altered (Table 2, effect 12), or where the spatial extent of habitat areas renewed is changed (Table 2, effect 13).

An example of the effect of the frequency of a habitat dynamic (Table 2, effect 12) is provided by modelling work of Lawson *et al.* (2010). Using a spatially explicit population model they tested the effects of fire interval, habitat loss and climate change on populations of a fire-dependent shrub (*Ceanothus verrucosus*, Nutt.). Fire resets succession and simultaneously causes seeds to germinate. Lawson *et al.* found that fire intervals of 35–50 years led to increases in expected minimum population abundance, whereas more or less frequent fires intervals decreased abundance. There was also an interaction between fire frequency and the severity of climate change, which altered whether certain fire frequencies were expected to have positive or negative effects on abundance. Thus, there were clear interactions (affecting abundance) between the pace of habitat dynamics and the climate scenario, which acted through expected future habitat availability. The work did not include a direct effect of climate on fire frequency, which may also change but also depends on fire management.

Habitat dynamics may also produce episodes of propagule dispersal. For instance, the *Daphnia* example (Altermatt *et al.* 2008) in the previous section shows how the drying of pools may lead to wind dispersal of dormant propagules. Warmer and drier summers led to greater rates of colonization of empty pools as dry pools that produced dormant propagules would also have increased. The system represents an interesting balance between the need for rainfall to fill pools but dispersal being more likely under drier conditions, so likely spring and summer rain (and temperatures) have different effects on both habitat dynamics and the colonization of pools. Whether the pace or scale of habitat dynamics changes because of climate change is a more open question.

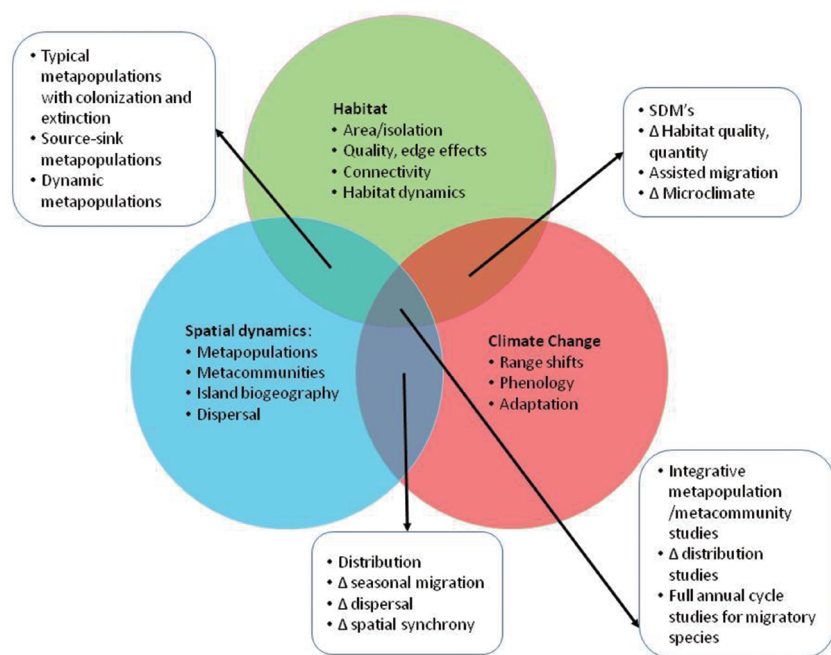
A potential example involving the altered spatial scale of a habitat dynamic (Table 2, effect 13) is also provided by changes in fire regimes. Many species are fire dependent and if the frequency of fire is changed, which is likely to happen in some areas if fire management regimes do not also change, then we would expect effects on persistence. Bachman’s sparrow [*Peucaea aestivalis* (Lichtenstein, 1823)] is a songbird that uses recently burned areas of pine forest in the south-east of the USA. The species feeds and nests on the ground and is most abundant in larger areas which have been burned within the past three years (Jones *et al.* 2014). Pulliam *et al.* (1992) show that in South Carolina the species has a source–sink metapopulation structure and point to the

need for forest management to consider spatial patterns both for occurrence and for future dispersal. Clearly, if fire regimes change there is a need to also consider climatic factors.

These examples illustrate a few ways that habitat dynamics may be affected by climate. There is a clear need to focus on how habitat formation and destruction processes depend on climate and to consider the effects through a variety of mechanisms. Such mechanisms include effects on the quality and quantity of habitat, modifying habitat connectivity, creating temporally pulsed dispersal, and direct effects on both extinction of local populations and on creating new habitat patches that are available for colonization.

## FUTURE OPPORTUNITIES AND RESEARCH NEEDS: A CALL FOR INTEGRATIVE STUDIES

The framework we present here elucidates that understanding the effects of climate change on habitat fragmentation involves intersecting ecological climatic effects with those of habitat effects on species (e.g. quality, quantity and dynamics) and spatial dynamics (e.g. dispersal, extinction and colonization). Figure 2 summarizes a sampling of the kinds of ways that ecologists study these factors and their interaction. For



**Figure 2** Venn diagram showing how ecologists study habitat effects, ecological effects of climate change and spatial dynamics. The  $\Delta$  symbol is used to indicate “change.” SDM indicates species distribution models, which are used to relate species’ occurrences to habitat (and environmental) conditions. “Dynamic metapopulations” imply that habitat is dynamic as well as populations turning over within patches (e.g. Hastings 2003).

instance, source–sink dynamics represent an interaction between habitat effects (habitat-specific demography) and spatial dynamics (rescue effects). Not surprisingly, because it is hard to study spatial population dynamics and the effects of habitat fragmentation, studying the effects of climate change on them is difficult. Thus, the challenge is to find studies that do jointly consider spatial dynamics, habitat effects and climate change (the center portion of Figure 2).

Here we provide a sampling of areas of study where integration of this sort has been attempted, ways these attempts could be improved on and distinct areas of ecological study that might be especially amenable to such integrative work.

### Empirical tests of highly integrative models

The best examples to date of studies that jointly consider spatial dynamics, habitat effects and climate change come from integrative metapopulation models that include both habitat and demographic (or population dynamic) effects. For instance, the examples described above from Carroll (2007), Anderson *et al.* (2009), Lawson *et al.* (2010) and Fordham *et al.* (2013) all use models that create such integration. The potential value of such models is to connect the effects in Table 2 to either local population dynamics, dispersal or both in precise quantitative ways.

There is a need to take the findings of such models and test them empirically. For example, in the volcano rabbit studies by Anderson *et al.* (2009), one could further test whether habitat change is occurring and at what rate, to ascertain whether future habitat is likely to be available in areas where the habitat is not currently suitable. Carroll (2007) predicted interactions between factors such as climate change and habitat loss, or hunting and habitat loss; these models could be empirically tested by exploring the demography of populations in areas that differ in climate or hunting pressure. Such antagonistic effects have been found in empirical studies of patch occupancy (e.g. Mantyka-Pringle *et al.* 2012), but whether these effects have an effect on the dynamics of metapopulations (as opposed to occupancy patterns) also merits testing. In studies that do use models it is also important to describe the effects of the different factors in a transparent way because sometimes we are left with the author's/authors' words for what the mechanism of change is without it being clear from the results presented. Therefore, it is important to document results in ways that make the underlying drivers and dynamic mechanisms clear.

Doing so is likely to lead to more critical tests and will help to generalize effects across studies.

### Population synchrony and the role of climatic drivers of population dynamics

The Moran effect (Moran 1953; Hudson & Cattadori 1999) provides a mechanism for how populations with a similar density dependent structure may be synchronized by environmental perturbations. Such spatial synchrony in population fluctuations is extremely widespread, and it is recognized that synchrony may reduce the potential for rescue effects where immigration forestalls extinction of a population, or for predators to reach areas with more abundant prey (Liebhold *et al.* 2004). The kinds of climatic events that can synchronize populations vary across taxa. For instance, for insects widespread droughts may do so (e.g. Hawkins & Holyoak 1998), whereas for small land birds severe winter weather may be more relevant (e.g. Bellamy *et al.* 2003). So the question is whether such events and others that might synchronize populations are changing in frequency because of climate change. We have a high degree of confidence that variation in temperature has increased, but severe winter weather has also declined in frequency (Hartmann *et al.* 2013) so the net effect is not clear and likely varies among regions. We have only low to medium confidence that droughts have increased in frequency (Hartmann *et al.* 2013), and some reports indicate that drought increases in the last century are not abnormal within the last millennium (Cook *et al.* 2004). The future frequency of many recurrent environmental events that are somewhat predictable, such as fires, floods, windstorms and ice storms, is somewhat unknown, but all could have large impacts on ecological systems (e.g. Dale *et al.* 2001). It is not clear whether even more extreme environmental events, such as hurricanes, are increasing in frequency because their rarity makes them hard to study (Hartmann *et al.* 2013). Overall, we need further study of whether ecologically-relevant climate drivers are changing in frequency or intensity, and what this does to population dynamics, spatial synchrony and spatial dynamics more generally. Considering the intersecting effects in Figure 2 might lead us to ask whether changed synchrony is a result of effects on habitat, direct effects of climate or altered dispersal. Thinking of spatial dynamics, does increased synchrony lead to a loss of rescue effects so that sink populations are likely to become extinct? Some of these are age-old questions, but the imperative for their study is increased by climate change.

## **Tying phenological changes to population dynamics**

While changes in phenology due to climate change are the most frequently reported climate-change effects (Parmesan 2006), rather few studies have looked at consequences for population dynamics, spatial or otherwise. Both *et al.* (2006) report that nesting pied flycatchers [*Ficedula hypoleuca* (Blyth, 1843)] have advanced their breeding at European sites with the greatest warming, and that flycatcher populations declined the most when food (caterpillar population) peaks were earlier or egg-laying dates were later. Visser and Both (2005) suggest that the timing of activity relative to peak food abundance is an appropriate measure of how much phenology should change if a species is to adapt to climate change and avoid negative fitness consequences. They found that for examples covering phenological pairs, such as zooplankton and algae, plants and insects, and insects and birds, observed phenological shifts were too little in 5 of 11 cases and too large in 3 of 11 cases for peak food timing to match peak consumer timing. The lack of studies examining the consequences of such shifts for spatial population dynamics is surprising considering the large number of studies that document phenological shifts (Parmesan 2006).

## **The spatial dynamics of species interactions under climate change**

While this review has concentrated on autecological effects it has been hard to avoid considering species interactions, in part because host plant species may be required for food resources or pollinators for plant sexual reproduction, and species that serve these functions are also frequently changing because of climate change. There have been a few proposed frameworks for considering interacting species' responses to global climate change (e.g. Tylianakis *et al.* 2008; Gilman *et al.* 2010). Not many patterns are consistent across species or groups of species. Tylianakis *et al.* (2008) suggest that mutualisms like pollination and seed dispersal tended to be uniformly negatively impacted by climate change. Schweiger *et al.* (2008) and Gilman *et al.* (2010) suggest that trophic specialists are more at risk from climate change than trophic generalists. Compared to generalists, specialists may have additional vulnerability because of dependence on another species for, for instance, food, and that species may be dispersal or climate limited.

Gilman *et al.* (2010) cite some examples of species that are especially vulnerable because the resource (or other partner) species might have different physiological tolerances or dispersal. Data are particularly needed on how the degree of specialization and dispersal vary. An example of within-species variation in specialization and dispersal is Tengmalm's owl (*Aegolius funereus* L., 1758) in Europe. The species is nomadic and more specialized in diet in the northern part of its range, and is a diet generalist that exhibit partial migration and residency in the southern part of its range (Korpimäki 1986). However, the problem of fitting movement patterns in with diet is more complex than a simple generalism–specialism axis, as exemplified by migratory *Sylvia* warblers that eat fruits prior to and during migration (Jonzén *et al.* 2011), or seed-eating passerine birds that switch to insectivory during breeding. More generally, there is a need to seek commonalities in how species interactions are altered by climate and what effect spatial dynamics has on these interactions.

## **Seasonal migration and spatial dynamics**

A general need in population ecology is to study species that are seasonal migrants year-round, to overcome the problem that most studies take place in species' breeding grounds at the expense of migratory patterns and population dynamics in wintering areas (Marra *et al.* 2015). In general, seasonal migration represents a reaction to adverse conditions, and its drivers may vary among taxonomic groups or geographically. For instance, while North American and European land birds show relationships between the proportion of migrants and latitude indicating winter weather (Newton & Dale 1996a,b), the proportion of migratory Australian butterflies show relationships with rainfall alone (Dingle *et al.* 2000). Given the more geographically uniform trends expected for temperature than for rainfall, we might expect that birds show stronger trends in migration timing or occurrence than do butterflies. However, as Winkler *et al.* (2014) point out, the mechanisms by which species respond to environmental cues will necessarily lag behind climate change because selection operates as a result of the decisions made. Consequently seasonal migrants may be especially vulnerable to the negative effects of climate change, in part because of phenology (above), and also because of increases in weather variation (Hartmann *et al.* 2013). Conversely, migrants may have flexible strategies, such as moose (*Alces alces* L. 1758) reducing their migratory behavior when snow is deeper

(Singh *et al.* 2012). Partial migration, where only some individuals or age classes migrate, also occurs, which gives variation on which selection may act and allow species to adapt to changed seasonality (Lundberg 1988).

We can think of seasonal migration from the perspective of how migrants find appropriate areas in unfavorable seasons (e.g. Knudsen *et al.* 2011), but migrants may also be negatively impacted by changing climate and habitat conditions in wintering (or unfavorable season) areas. Areas and/or habitats in which European birds winter have been linked to population declines: Ockenden *et al.* (2012) analyzed patterns of decline in 26 species of Afro-Palearctic migrant and found that arid-zone wintering species declined less than those wintering in southern Africa or humid tropical areas of central and western Africa. On average, species occupying open and woodland habitats declined, whereas habitat-generalist species increased in abundance. This led the authors to conclude that migration was constrained, such that these species lacked a plastic ability to move to other wintering areas and habitats. Robbins *et al.* (1989) found that 20 species of Neotropical migrant songbirds demonstrated significant population declines from 1978 to 1987 and that while species using interior forested habitats in winter showed declines, those using scrub habitats in winter showed increases (Robbins *et al.* 1989). Other bird species have declined because of low rainfall in wintering or migration passage areas in West Africa (see Szep 1995 and references therein).

Finally, migratory species may experience spatially and temporally distinct climate change impacts during different phases of their annual cycle, with one having potential carry-over effects to the next (Small-Lorenz *et al.* 2013). One key link between wintering and breeding grounds for migratory species is migratory departure and arrival times, and there is evidence that climate and habitat change can influence timing above and beyond the deterministic endogenous cues of photoperiod. For example, Studds and Mardra (2011) demonstrate the effects of winter habitat type, and later winter rainfall and food availability, on the spring departure dates of American redstart (*Setophaga ruticilla* L., 1758) individuals in Jamaica; birds departed wintering grounds earlier in mangrove versus second-growth scrub habitats in years of more versus less rainfall and in sites with more arthropod biomass. Further studies of migration patterns, areas and timing are clearly needed (Knudsen *et al.* 2011), and more generally we need to tie different

parts of annual life-cycles together to obtain a complete picture of annual population dynamics (Marra *et al.* 2015).

### The spatial dynamics of nomadic species

Nomadism is generally characterized by extreme spatiotemporal variation, with nomads sometimes not recurring within a location for many years, and is frequently linked to rainfall and productivity in arid environments (Wiens 1989). Although nomadic species are difficult to study because of their wide area of potential occurrence and infrequent occurrence in any one place, their response to climate change is of interest and relevant here because of the extreme spatial dynamics they exhibit. Frequently in ecology, reactions to extreme conditions help to explain general mechanisms. Desert waterbirds represent an extreme of species that are stochastic in time and widely distributed in space in response to habitats characterized by low and highly variable rainfall (e.g. Roshier *et al.* 2008; Pedler *et al.* 2014). Banded stilts [*Cladorhynchus leucocephalus* (Vieillot, 1816)] in Australian deserts represent an extreme even compared to most desert waterbirds, and have been recorded moving up to 2200 km in 2.5 days in search of ephemeral salt lakes that become productive wetlands after rain (Pedler *et al.* 2014). Some birds dispersing from ponds that were drying out moved across the entire continent of Australia before settling on other water bodies. Movement behaviors included both ranging (short flights out from a water body and then returning) and long-distance directed flights (Pedler *et al.* 2014). How birds detect flooded areas is an open question. Pedler *et al.* (2014) suggest that some birds moved to areas following large rainfall and flooding events, and suggested possible detection of distant weather systems through low-frequency sound, or temperature or pressure gradients. Other flights took place weeks after rainfall events, perhaps in response to odor cues (Pedler *et al.* 2014). The variety of strategies of movement within this species and other nomads perhaps indicate that such species are very flexible in their ability to deal with climatic variation. However, they could also be viewed as already living a tenuous existence and so further aridity might drive them to extinction. For such reasons, nomadic species merit further investigation.

### CONCLUDING REMARKS

To close, we advocate the integration of direct and indirect effects of climate change while thinking

laterally about changes in habitat, movement in all its forms, habitat dynamics, phenology and spatial synchrony. Shifts in timing, distribution, habitat dynamics and synchrony represent a mix of responses of species to climatic changes and may produce further feedbacks operating through individual biological and population changes. Climatically-induced individual-level biological changes span physiology, behavior, life-history and demography. At a population level, feedback processes of density and frequency dependence alter responses to environmental drivers; for instance, altered spatial synchrony modifies the ability of organisms to move to experience different population conditions. As we have outlined and catalogued, integrative modeling and empirical studies, further consideration of phenological effects, and integration of different parts and locations of annual life-cycles are required to fully understand spatial dynamic responses to climate change in diverse taxa.

## ACKNOWLEDGMENTS

M. Holyoak was funded by a Hatch fund project. SK Heath was funded by a UC Davis Graduate Group in Ecology Fellowship.

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**Cite this article as:**

Holyoak H, Heath SK (2016). The integration of climate change, spatial dynamics, and habitat fragmentation: A conceptual overview. *Integrative Zoology* **11**, 40–59.