



# Facilitating climate-change-induced range shifts across continental land-use barriers

Cassandra M. Robillard,\* Laura E. Coristine, Rosana N. Soares, and Jeremy T. Kerr

Canadian Facility for Ecoinformatics, Department of Biology, University of Ottawa, 30 Marie Curie Pvt, Ottawa, Canada K1N6N5

**Abstract:** *Climate changes impose requirements for many species to shift their ranges to remain within environmentally tolerable areas, but near-continuous regions of intense human land use stretching across continental extents diminish dispersal prospects for many species. We reviewed the impact of habitat loss and fragmentation on species' abilities to track changing climates and existing plans to facilitate species dispersal in response to climate change through regions of intensive land uses, drawing on examples from North America and elsewhere. We identified an emerging analytical framework that accounts for variation in species' dispersal capacities relative to both the pace of climate change and habitat availability. Habitat loss and fragmentation hinder climate change tracking, particularly for specialists, by impeding both propagule dispersal and population growth. This framework can be used to identify prospective modern-era climatic refugia, where the pace of climate change has been slower than surrounding areas, that are defined relative to individual species' needs. The framework also underscores the importance of identifying and managing dispersal pathways or corridors through semi-continental land use barriers that can benefit many species simultaneously. These emerging strategies to facilitate range shifts must account for uncertainties around population adaptation to local environmental conditions. Accounting for uncertainties in climate change and dispersal capabilities among species and expanding biological monitoring programs within an adaptive management paradigm are vital strategies that will improve species' capacities to track rapidly shifting climatic conditions across landscapes dominated by intensive human land use.*

**Keywords:** adaptive management, climate change, corridors, fragmentation, habitat loss, monitoring, refugia

Facilitar los Cambios en las Extensiones Inducidos por el Cambio Climático a lo Largo de Barreras Continentales de Uso de Suelo

**Resumen:** *Los cambios climáticos imponen requerimientos a muchas especies para que cambien sus extensiones con tal de permanecer dentro de las áreas tolerables ambientalmente, pero las regiones casi continuas de uso de suelo intenso por humanos, que se extienden a lo largo de extensiones continentales, disminuyen los prospectos de dispersión para muchas especies. Revisamos el impacto de la pérdida de hábitat y la fragmentación sobre la habilidad de las especies para rastrear climas cambiantes y también los planes existentes para facilitar la dispersión de especies en respuesta al cambio climático en regiones de uso intensivo de suelo, partiendo de ejemplos de América del Norte y otros lugares. Identificamos una marco analítica emergente que toma en cuenta la variación en las capacidades de dispersión de las especies con relación al ritmo del cambio climático y la disponibilidad de hábitat. La pérdida de hábitat y la fragmentación dificultan el rastreo del cambio climático, particularmente para las especies especialistas, al impedir la dispersión de propágulos y el crecimiento poblacional. Nuestra marco analítica identifica refugios climáticos posibles en la era moderna, en los cuales el ritmo del cambio climático ha sido más lento que en las áreas circundantes y los cuales están definidos en relación con las necesidades individuales de las especies. La marco enfatiza la importancia de identificar y manejar las vías de dispersión o corredores que atraviesan barreras semi-continentales de uso de suelo y que pueden beneficiar a muchas especies simultáneamente. Estas marcos emergentes para facilitar los cambios en la extensión deben tomar en cuenta las incertidumbres que rodean la adaptación poblacional a las condiciones ambientales locales. Tomar en cuenta las incertidumbres en el cambio climático*

\*Address correspondence to Cassandra M. Robillard, email [crobi021@uottawa.ca](mailto:crobi021@uottawa.ca).  
Paper submitted November 6, 2014; revised manuscript accepted May 28, 2015.

*y las capacidades de dispersión entre las especies y expandir los programas de monitoreo biológico dentro del paradigma de trabajo de manejo adaptativo son estrategias vitales que mejorarán las capacidades de las especies para rastrear rápidamente las condiciones climáticas cambiantes a lo largo de paisajes dominados por el uso de suelo antropogénico intensivo.*

**Palabras Clave:** cambio climático, corredores biológicos, fragmentación, manejo adaptativo, monitoreo, pérdida de hábitat, refugios biológicos

## Introduction

While rapidly changing climates elevate extinction risk (Maclean & Wilson 2011), habitat loss and degradation continue to pose severe threats to many species (Vié et al. 2009; Collen et al. 2012). Across North America, intensive and extensive land uses have eliminated or degraded critical habitats in many of the most biologically diverse areas. The result is that rates of species endangerment in such areas are high (Brown & Laband 2006). Anthropogenic climate change poses an independent array of risks that may interact with habitat loss impacts to accelerate extinction rates still further. Although mechanisms governing how, why, and when species respond to changing climatic conditions continue to be discovered (Araujo et al. 2013), strategies to reduce population and species extinctions arising from habitat losses or degradation must clearly account for directional shifts in the underlying environmental factors that often determine the limits of species distributions.

Climate change imposes requirements for geographical range shifts for many species, but land use conversions across broad regions in North America impose a potential dispersal barrier spanning much of the continent (Fig. 1). Anticipated warming of 2–5 °C in the next century over this region (IPCC 2013) adds to the complexity of conservation planning, the effectiveness of which will depend in part on the extent to which the impacts of habitat loss and climate change, respectively, and interactively, can be mitigated. We reviewed the impact of habitat loss and fragmentation on species' abilities to track changing climates. The review focused on the highly developed regions of eastern and central North America as a hotspot for these interactions, and human footprint, a metric of human influence (Sanderson et al. 2002), was assessed within latitudinal bands across North America to illustrate this variation in human-imposed barriers to dispersal. We then reviewed the systematic conservation planning, ecology, and evolution literature for existing conservation planning and management approaches that facilitate species dispersal in response to climate change through regions of intensive land uses, as exemplified by cases in North America and elsewhere. Strategies to manage for changing land use intensities and climate change have evolved rapidly (e.g., Faleiro et al. 2013; Alagador et al. 2014) and have begun to account for an increasingly mechanistic understanding of the factors

that govern species' ecoevolutionary and phenotypic responses to complex global change threats (Hoffmann & Sgro 2011).

## Climate Change, Range Shifts, and Habitat

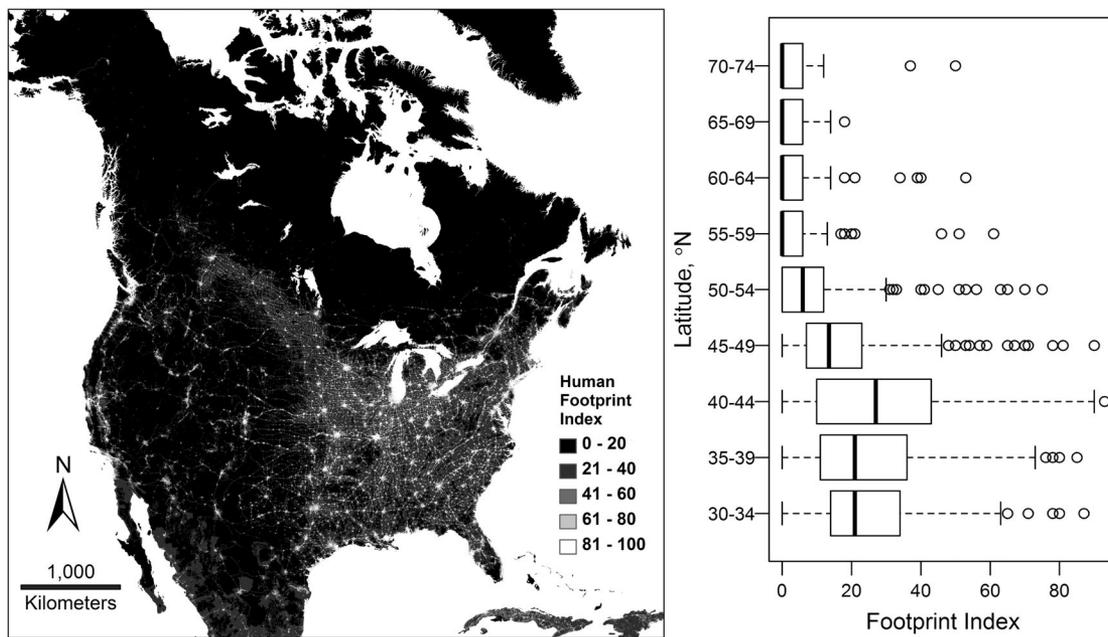
The successful expansion of a species' range at the cold range margin depends on the presence of habitat that may be colonized by individual dispersal. Shifts in species' distributions can be modeled as propagule diffusion within a window of suitable climate that moves across a landscape as climates change (Travis 2003; Leroux et al. 2013). Species' distributions must keep pace with this moving climate window to avoid accumulation of climate debts and potentially extinction (Devictor et al. 2012) by colonizing new areas at expanding range margins even as individuals of populations are lost from retracting warm margins. A species' ability to keep pace depends on its rate of spatial spread, itself a function of individual movement rates and the population growth rate. In mathematical terms, this rate of spread can be modeled by

$$c^* = 2\sqrt{Dr}, \quad (1)$$

where  $c^*$  is the critical rate of spread for tracking the suitable climate,  $D$  is the diffusion rate of individuals or rate of individual movement, and  $r$  is the population growth rate (Leroux et al. 2013). As part of this emerging reaction-diffusion framework for modeling species movement, it is possible to generate predictions for the minimum critical size of a patch of habitat that will permit species persistence, given that both the patch and the species must shift with respect to changing climatic conditions:

$$L_C(q) = \pi\sqrt{D/r} \left( \sqrt{1 - \frac{q}{2\sqrt{Dr}}} \right)^{-1}, \quad (2)$$

where  $L_C$  is the minimum critical size of the species' climatic envelope (or area that is climatically tolerable), which moves at pace  $q$ . It is then straightforward to show that species persistence depends on whether its rate of movement,  $c^*$ , is at least equal to the rate of movement of its tolerable climate,  $q$ . This framework predicts which species will be at risk from climate change, given knowledge of their dispersal rates and observations of shifts in their areas of climatically tolerable habitat, providing a means to include more mechanistic insights into



**Figure 1.** Human footprint in North America, expressed as a percentage of the human influence present in each terrestrial biome, measured with a combination of data on population density, human land use and infrastructure, and human access via waterways, rail, and roads (derived from Sanderson et al. [2002]). Graph shows median footprint (vertical lines) and interquartile range of footprint values (boxes) relative to latitude (dashed lines, most extreme data point within 1.5 times the interquartile range; circles, outliers). Although footprint appears to be concentrated on the eastern half of the continent, there is a clear peak through the middle of the continent, stretching through central Canada to the Rocky Mountains in the west.

how dispersal affects range shifts due to climate change (developed in Leroux et al. [2013]).

Species' range responses to changing climatic conditions depend on their capacity to disperse (Boulangéat et al. 2012), which relates to habitat availability and connectivity (Leroux et al. 2013). Range expansion predictions for the speckled wood butterfly *Pararge aegeria* that included growth rates and a dispersal function accurately predicted the observed difference in range expansion rate between a habitat-rich landscape and a fragmented, habitat-poor landscape (Hill et al. 2001). Cropland (Janin et al. 2009; Ockinger et al. 2012), clearcuts in forested landscapes (Popescu et al. 2012), and urban or built areas (Tremblay & St Clair 2011; Sackett et al. 2012) are pervasive in much of North America (Fig. 1) and inhibit the movement of individuals or reduce colonization success in remaining habitat patches for butterflies, toads, songbirds, and prairie dogs. Even for species requiring structurally similar habitats to those that agricultural land uses replaced, such as for grassland species remaining in areas of high-productivity cropland, fragmentation from various land uses isolates populations (Soons & Heil 2002; Torok et al. 2011) and is linked to persistent bird population declines (Sauer et al. 2003). Habitat loss is particularly likely to diminish dispersal capacities of habitat specialists, making it less likely that such species will track shifting climatic conditions

successfully (Warren et al. 2001; Travis 2003; Stefanescu et al. 2011). Because intensive land uses effectively filter these species out of changing biological communities and generalists persist more readily or expand their distributions, this land use and climate change interaction accelerates biotic homogenization over broad regions (White & Kerr 2007).

## Designing Reserve Networks for Range Shifts

Alleviating habitat loss will both reduce its biotic impacts directly and improve prospects that species dispersal rates will suffice to track shifting climatic conditions (Heller & Zavaleta 2009; Lemieux et al. 2011). Although the continued efficacy of formal protected areas in the face of changing climates and shifting ranges is uncertain (Kharouba & Kerr 2010; D'Amen et al. 2011; Kujala et al. 2011; Johnston et al. 2013), creating and maintaining protected areas continues to be essential for conservation strategies that address climate change because they mitigate other human impacts (Hannah et al. 2007; Lemieux et al. 2011). However, the strategy of prioritizing potential reserves based on species' current distributions is clearly limited by increasingly dynamic species distributions (Williams & Jackson 2007; Hobday 2011); additional, innovative strategies are urgently needed.

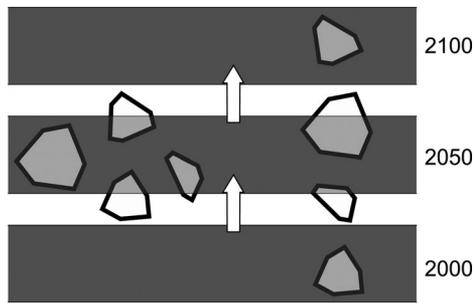


Figure 2. A conventionally clustered reserve network (left) and a reserve network stretched along the axis of climatic niche movement (gray, climate windows at 3 periods intended to exemplify significant climate change; arrows, direction of climate window movement).

### Protection along Climate Change Trajectories

Species' capacities to track shifting climates depend strongly on availability of sufficient habitat where species can establish populations beyond their historical range limits and subsequently disperse (Hiley et al. 2013). Protecting or restoring habitat that strategically facilitates range shifts (effectively increasing the  $c^*$  term and diminishing the risk of  $q > c^*$  in Eq. (2)), such as in areas that are poleward or upslope of existing range boundaries or biodiversity hotspots, will reduce extinction risks related to climate change. This creates a unique challenge for conservation planners because a reserve may be only transiently tolerable for constituent species. Although many climatic generalist species will continue to benefit from existing reserve networks, other species may need to use those reserves to shift through landscapes where habitat losses might otherwise hinder or prevent dispersal. If so, arranging individual reserves or managed lands along the expected trajectories of shifting species' niches will improve their likelihood of colonizing new areas (Fig. 2) (Lawler 2009; Alagador et al. 2014).

Managing habitats along the trajectory of distribution changes requires prediction of this trajectory in a landscape. For North America east of the Rockies, the trajectories of climate change are largely northward; some converge toward higher elevations such as the Appalachian ranges and along northern coastlines (Burrows et al. 2014). However, observations of how climatic niches have shifted across landscapes can provide greater insight than direction and pace; multiple trajectories can be mapped to identify the timing and extent to which these trajectories converge, remain overlapping, and diverge. For example, the pace of climate change has been calculated (Loarie et al. 2009). From these calculations, 50-year trajectories (1960–2009) of climatic niches have been mapped across North America that identify climate “corridors,” where many of these trajectories pass through a single common region (Burrows et al.

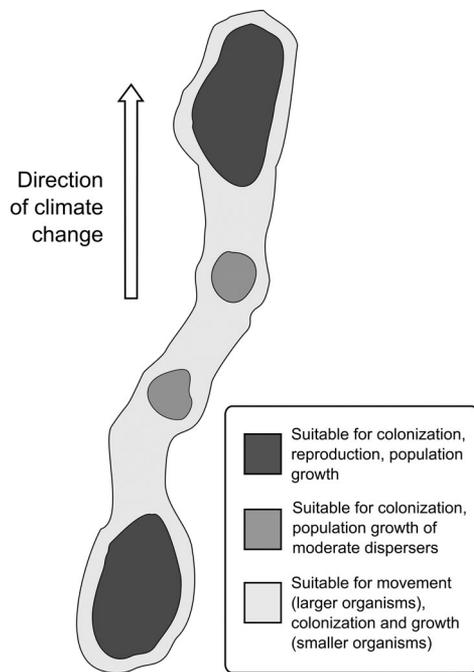
2014). If species are expected to track individual climatic niches in a shared direction (if not pace), these common routes of migration imposed by climate change need identification and management. Although geographical range shifts observed to date have not yet been strongly limited by hard geographical boundaries, such as coastlines, region-specific management will be necessary to account for such responses in some areas (e.g., California [Ackerly et al. 2010]).

Predicting species distributions based on models of future climate (Pyke et al. 2005; Rose & Burton 2009; Kujala et al. 2013b; Loyola et al. 2013) relies on many assumptions (e.g., that the current distributions of species are in equilibrium with climate) or on underlying models with their own assumptions and uncertainties (e.g., about future CO<sub>2</sub> emissions [Buisson et al. 2010]). The accuracy of these predictions is infrequently tested (Crimmins et al. 2013). It is important to validate such models by testing their ability to predict changes over periods of observed climate change (Kharouba et al. 2009; Kerr & Dobrowski 2013; Williams et al. 2013). Finally, shifting climatic niches are not necessarily geographically continuous (Early & Sax 2011), which creates gaps along dispersal pathways that may lead to more complex management requirements.

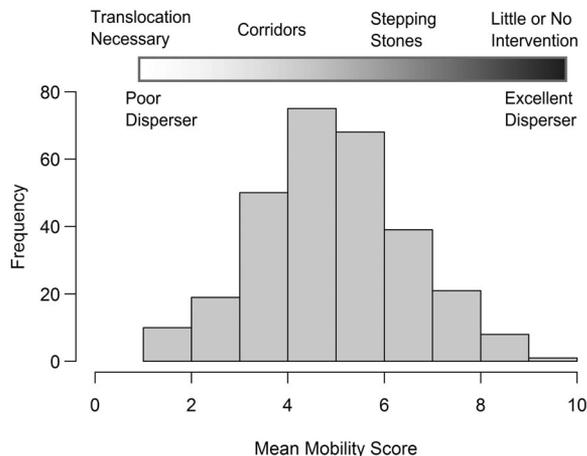
### Connectivity through Corridors, Stepping-Stones, and Translocation

The distribution of dispersal characteristics among species assemblages can inform the nature of potential management interventions. Range shifts in response to climate change are contingent on successful individual dispersal among habitat patches, the probability of which can vary regardless of landscape permeability. Strategies to connect conservation areas must account for potentially enormous variation in target species' intrinsic dispersal abilities (Burke et al. 2011). Some species will successfully disperse through even extremely fragmented landscapes, whereas other species will not disperse rapidly enough to track shifting climatic conditions even if habitats are nearly continuous and subject only to natural disturbances. Among species for which long distance dispersal is unlikely, for example, corridors may be needed (Beier et al. 2008), whereas habitats arrayed as stepping-stones may suffice for species that disperse over moderate distances relative to existing geographical barriers (e.g., wind- or bird-dispersed seeds) (Fig. 3) (Pearson & Dawson 2005). As a result, strategies to improve connectivity in human-dominated landscapes may range from no intervention at all to managed relocation (Pearson & Dawson 2005; Shoo et al. 2013).

New techniques are required to assemble and evaluate dispersal capacities within large species assemblages and



**Figure 3.** Two ways to connect habitat patches (black) for species tracking climate niches moving from bottom to top of the figure: continuous corridors (light grey) and stepping-stones (dark grey).



**Figure 4.** Butterfly mobility scores (derived from Burke et al. [2011]) and best approaches for habitat connectivity based on dispersal ability.

to evaluate methods to facilitate their dispersal across human-impacted landscapes. Burke et al. (2011) assembled consensus of expert views on species' mobility for 297 butterfly species in United States and Canada, which showed that dispersal capacities varied enormously among species. Some of these species are unlikely, without some form of management intervention (Fig. 4), to keep pace with shifting climatic conditions. Interventions to facilitate such geographical range shifts

vary relative to species intrinsic dispersal capacities, ranging from no intervention to managed relocation, as well as local land uses and costs. Corridor or stepping-stone establishment, through formal protection measures or informal land use management, will often be less intrusive and potentially less costly than managed relocation, depending particularly on whether these landscape features are being retained or must be restored (Hoegh-Guldberg et al. 2008; Shoo et al. 2013). The costs and logistical difficulty of managed relocation increase rapidly as numbers of species requiring relocation increase (Loss et al. 2011), although prohibitively high land costs or inflexible land uses may sometimes make managed relocation relatively economical.

Connectivity is particularly relevant to trans-national conservation issues. In North America, for instance, human-dominated regions of eastern and central North America extend across the border between Canada and the United States and maintenance of landscape connectivity in trans-boundary areas requires international cooperation. There is some precedent for international cooperation in the Great Lakes watershed, through long-standing activities of the International Joint Commission (Hall 2008). Broad-scale initiatives of this kind are similarly exemplified by the Yellowstone to Yukon (Raimor & Ford 2005) and Algonquin to Adirondacks (Stephenson 2001) corridors, but they remain uncommon. Such efforts may need to be expanded particularly in central North America, where the pace of climate change is higher (Loarie et al. 2009) and species consequently experience greater challenges in tracking shifting climatic conditions. Building cooperative management structures between agencies and governments with limited histories of trans-boundary co-operation may be challenging but will likely be indispensable.

### Climatic Refugia

Strategies to reduce the geographical displacement rates of species' climatic niches provide potentially vital benefits that complement widely recognized approaches of facilitating dispersal through human-dominated landscapes. During past climate changes, paleoecological and phylogeographic data indicate that small populations of many species sheltered successfully in climatic refugia and subsequently expanded as climatic conditions allowed (Svenning et al. 2008; Hampe et al. 2013). Identifying similar areas that could buffer impacts of current anthropogenic climate change is an urgent requirement (Ashcroft 2010; Dobrowski 2011; Keppel et al. 2012; Reside et al. 2013). The capacity of a site to act as a refugium depends on the rate of warming within it relative to surrounding areas, the duration and magnitude of climate change, and climatic tolerances of resident biota (Moritz & Agudo 2013).

Biological mechanisms governing species' responses to climate change can inform efforts to identify modern climatic refugia. If these areas are defined as having lower rates of climate change, refugia effectively reduce the rates at which species' climatic envelopes ( $q$ , or tolerance niches sensu Sax et al. [2013]) move relative to species' dispersal rates ( $c^*$ ). Refugia complement strategies intended to increase species dispersal rates because those rates are measured relative to how quickly areas with suitable climates shift. All other things being equal, the most effective refugia will be relatively large so as to reduce risks of localized, stochastic extinctions and mitigate climate impacts sufficiently well that  $q < c^*$  for the duration of the climate change period. In principle, this means refugia can satisfy their technical definition while being spatially dynamic; that is, they act like a habitat corridor that is buffered against climate change impacts. This issue has been little explored (Graham et al. 2010; Rose & Burton 2011). Although the roles of refugia in preserving relictual populations during periods of sustained cooling is well known (Hampe et al. 2013; Jurickova et al. 2014), their durability during periods of rapid warming is considerably less certain. Expanded understanding of the distribution and dynamics of refugia relative to recent climate changes and potentially constituent species is urgently needed.

## Local Adaptation and Dispersal

A population is more likely to survive the effects of climate change if it retains sufficient standing variation to enable adaptive shifts in tolerance of changing environmental conditions. These effects are ubiquitous, given that even very long-lived species, such as trees, show widespread evidence of local adaptation to climatic conditions (Davis et al. 2005; Franks et al. 2014). Furthermore, local adaptation to climatic conditions depends on the balance between local selective responses and gene flow (Lenormand 2002), which may shift rapidly in areas where human land uses impose dispersal barriers but climate-change-related selective pressures vary spatially and temporally. Selection can nevertheless shift species' critical thermal limits to the extent that local genetic variation exists. *Drosophila* populations rapidly evolve increased tolerance to stressful abiotic conditions in experimental microcosms (Reusch & Wood 2007). Species' seasonal timing (phenologies) have shifted rapidly over recent decades (Kharouba et al. 2014), responses that reflect phenotypic plasticity and the presence of sufficient genetic variation to permit selection (Bertheaux et al. 2004; Bradshaw & Holzapfel 2008; Skelly & Freidenburg 2010). Similarly, variability in heat shock protein expression can be high, suggesting potential responses to strong selection for increasing upper critical

temperature (Reusch & Wood 2007). Conversely, recent reviews of thermal thresholds globally suggest there is strong conservatism across taxa in upper thermal limits (Araujo et al. 2013), and shifts in tolerance at species upper thermal limits occur much slower than at their lower thermal limits (Munoz et al. 2014). Maintenance of genetic diversity in support of traits that are critical for adaptive responses to warming (e.g., thermal tolerance), as well as identifying populations with limited adaptive potential (Hoffmann & Sgro 2011), would improve the prospects of successful conservation outcomes.

Yet, climate change may select for differences in dispersal ability, not just thermal tolerances. Warming along species' geographical range limits in fragmented landscapes selected for increased dispersal capacity among insect populations (Hill et al. 2011). In those areas, individuals with greater dispersal capacity would be the first to colonize areas that have newly become climatically suitable, allowing them to escape intraspecific competition (Hargreaves & Eckert 2014). In contrast, model-based expectations suggest that dispersal can reduce probability of successful adaptation to climate change by exposing species to novel competitors (Norberg et al. 2012). Apparent mismatches between model-based and field ecological observations can be substantial. However, there is emerging consensus that assisted gene flow or management activities that increase dispersal rates are likely to accelerate adaptation to changing climatic conditions, but negative impacts, such as outbreeding depression, also present risks that must be recognized and addressed (Sgro et al. 2011; Weeks et al. 2011).

While models that assume strong potential impacts of competition can predict negative impacts of dispersal on population survival, alternative theoretical frameworks have been described (e.g., Leroux et al. 2013) in which dispersal is critical to improve prospects for species survival. This framework was linked to field-based observations to generate predictions of risks related to climate change relative to species' dispersal capacities and climatic tolerances across large areas of North America. Risks associated with outbreeding depression, for instance, may prove larger in populations that are naturally highly fragmented, such as those inhabiting mountainous areas (Hamann & Aitken 2013). Across enormous areas of central North America, however, human land uses have subdivided formerly continuous landscapes that have very little topographical relief (see Fig. 1). Increasing dispersal rates among population isolates in such areas would restore gene flow to levels that could have been historically observed, which seems unlikely to yield perverse conservation outcomes in terms of adaptation, especially given the benefits of outcrossing for genetic rescue in isolated and inbred populations of naturally outbreeding species (Frankham 2015).

## Planning for Uncertainty

Anthropogenic climate change will impose non-analog conditions in some areas (Williams et al. 2007). These conditions will necessitate management of the effects of extreme events and species responses to previously unobserved environmental conditions (Lemieux et al. 2011). Large areas that include potential climatic refugia are more likely to provide both the shelter and resources species require under such circumstances. Agri-environmental programs used in Europe and the United States (Baylis et al. 2008) can maintain or improve habitat quality for target species within core protected areas and facilitate their dispersal through managed mixed use areas surrounding them (Donald & Evans 2006; Lawson et al. 2012). Accepted systematic conservation planning principles, such as redundant species representation within networks of protected or managed areas, will reduce the likelihood that climate changes will eliminate species from the system (Lemieux et al. 2011; Gillson et al. 2013). Smaller areas can help integrate networks that include widely dispersed large protected areas in regions adjacent to landscapes under highly intensive human use (Hannah 2011), such as across broad expanses of central North America.

To predict species responses to climate change in a way that allows effective targeted approaches (Heller & Zavaleta 2009; Dunlop et al. 2012), observations and mechanisms determining species' responses to recent changes are vital (Kujala et al. 2013a). Long-term monitoring programs (McMahon et al. 2011), such as the Breeding Bird Survey (Newman 2011; Sauer et al. 2013), provide measurements of species' responses against historical values. This temporal component provides context and considerably greater biological insight than purely spatial measurements (e.g., Kerr et al. 2007) and is critical if adaptive management (where best practices are determined "through sequential reassessment of system states and dynamic relationships" either actively through experimentation or passively through monitoring and experience [Rist et al. 2013]) is to employ the strongest evidence (Mawdsley 2011). Such management programs should also continue to monitor and manage populations of invasive species while recognizing the increasing difficulty of defining alien and native species in a changing world (Webber & Scott 2012).

## Conclusion

New research efforts that integrate mechanistic understanding of species' dispersal relative to the pace of climate change are vital to address conservation challenges posed by the interaction of high intensity human land use with rapid climate change. This framework also

provides the basis to identify modern climatic refugia, which can be viewed as areas with low rates of environmental change (or climate velocities) relative to species' dispersal abilities, a dynamic definition of *refugia* relative to anthropogenic climate changes. Although management strategies that account for biological variation in dispersal capacities that vary across species assemblages, such as assisted migration for species with the least dispersal capacity or where land costs prohibit use of other approaches, are likely to improve most species' conservation prospects, the same strategies also pose risks to populations that are locally adapted to environmental conditions. Uncertainties around impacts of extreme events and the advent of non-analog conditions, along with the need to account for and retain adaptive potential among target populations and species, represent important areas where research would yield practical benefits.

Some regions with large areas of intact wilderness remain, and strategies discussed here are intended to enable species to reach those areas successfully despite the presence of semi-continental dispersal barriers of intense human land use. Efforts to improve habitat for species in degraded areas are unlikely to yield perverse conservation outcomes, but wilderness areas outside these are also at risk. Extensive and rapid growth of industrial land uses, such as for bitumen oil extraction in the boreal landscapes just beyond North America's central plains, creates potentially impenetrable obstacles to geographical range expansion for some species as well as a growing footprint of comprehensive habitat destruction. This growth over the past decade is a reminder that the existence of expansive wilderness areas is no guarantee of their persistence. Such areas are also experiencing large climate change impacts and these generally grow larger toward the Arctic (IPCC 2013). Thus, species must become progressively better dispersers the further north their ranges extend, leading also to increasing relative impacts of land use changes on species capacities to track shifting climatic conditions in those areas. Wilderness conservation in these few frontier regions that remain must be a high priority. At the least, strategies that facilitate species movement beyond existing human-imposed dispersal barriers are likely to improve species' conservation chances during this epoch of accelerating climate change.

## Acknowledgments

We thank J. Zuloaga, B. Rayfield, and 2 anonymous reviewers for helpful comments on this manuscript. This work was supported by the Natural Sciences and Engineering Research Council (Discovery Grant Program, J.T.K.; Canada Graduate Scholarship, C.M.R.), the Ontario Graduate Scholarship Program (L.E.C.), the University Research Chair Program in Macroecology and Conservation

at the University of Ottawa (J.T.K.), and the University of Ottawa Excellence (L.E.C., C.M.R.) and Admission Scholarship Programs (R.N.S.).

### Literature Cited

- Ackerly DD, Loarie SR, Cornwell WK, Weiss SB, Hamilton H, Branciforte R, Kraft NJB. 2010. The geography of climate change: implications for conservation biogeography. *Diversity and Distributions* **16**:476–487.
- Alagador D, Cerdeira JO, Araujo MB. 2014. Shifting protected areas: scheduling spatial priorities under climate change. *Journal of Applied Ecology* **51**:703–713.
- Araujo MB, Ferri-Yanez F, Bozinovic F, Marquet PA, Valladares F, Chown SL. 2013. Heat freezes niche evolution. *Ecology Letters* **16**:1206–1219.
- Ashcroft MB. 2010. Identifying refugia from climate change. *Journal of Biogeography* **37**:1407–1413.
- Baylis K, Peplow S, Rausser G, Simon L. 2008. Agri-environmental policies in the EU and United States: A comparison. *Ecological Economics* **65**:753–764.
- Beier P, Majka DR, Spencer WD. 2008. Forks in the road: Choices in procedures for designing wildland linkages. *Conservation Biology* **22**:836–851.
- Berteaux D, Réale D, McAdam AG, Boutin S. 2004. Keeping pace with fast climate change: Can arctic life count on evolution? *Integrative and Comparative Biology* **44**:140–151.
- Boulangeat I, Gravel D, Thuiller W. 2012. Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecology Letters* **15**:584–593.
- Bradshaw WE, Holzapfel CM. 2008. Genetic response to rapid climate change: it's seasonal timing that matters. *Molecular Ecology* **17**:157–166.
- Brown RM, Laband DN. 2006. Species imperilment and spatial patterns of development in the United States. *Conservation Biology* **20**:239–244.
- Buisson L, Thuiller W, Casajus N, Lek S, Grenouillet G. 2010. Uncertainty in ensemble forecasting of species distribution. *Global Change Biology* **16**:1145–1157.
- Burke RJ, Fitzsimmons JM, Kerr JT. 2011. A mobility index for Canadian butterfly species based on naturalists' knowledge. *Biodiversity and Conservation* **20**:2273–2295.
- Burrows MT, et al. 2014. Geographical limits to species-range shifts are suggested by climate velocity. *Nature* **507**:492–495.
- Collen B, Böhm M, Kemp R, Baillie J. 2012. Spineless: status and trends of the world's invertebrates. Zoological Society of London, London.
- Crimmins SM, Dobrowski SZ, Mynsberge AR. 2013. Evaluating ensemble forecasts of plant species distributions under climate change. *Ecological Modelling* **266**:126–130.
- D'Amen M, Bombi P, Pearman PB, Schmatz DR, Zimmermann NE, Bologna MA. 2011. Will climate change reduce the efficacy of protected areas for amphibian conservation in Italy? *Biological Conservation* **144**:989–997.
- Davis MB, Shaw RG, Etterson JR. 2005. Evolutionary responses to changing climate. *Ecology* **86**:1704–1714.
- Devictor V, van Swaay C, Brereton T, Brotons L, Chamberlain D, Heliola J, Herrando S, Julliard R, Kuussaari M, Lindstrom A, et al. 2012. Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change* **2**:121–124.
- Dobrowski SZ. 2011. A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology* **17**:1022–1035.
- Donald PF, Evans AD. 2006. Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. *Journal of Applied Ecology* **43**:10.
- Dunlop M, Hilbert DW, Ferrier S, House A, Liedloff A, Prober SM, Smyth A, Martin TG, Harwood T, Williams KJ. 2012. The implications of climate change for biodiversity conservation and the national reserve system: final synthesis. CSIRO, Canberra.
- Early R, Sax DF. 2011. Analysis of climate paths reveals potential limitations on species range shifts. *Ecology Letters* **14**:1125–1133.
- Faleiro FV, Machado RB, Loyola RD. 2013. Defining spatial conservation priorities in the face of land-use and climate change. *Biological Conservation* **158**:248–257.
- Frankham R. 2015. Genetic rescue of small inbred populations: meta-analysis reveals large and consistent benefits of gene flow. *Molecular Ecology* **24**:2610–2618.
- Franks SJ, Weber JJ, Aitken SN. 2014. Evolutionary and plastic responses to climate change in terrestrial plant populations. *Evolutionary Applications* **7**:123–139.
- Gillson L, Dawson TP, Jack S, McGeoch MA. 2013. Accommodating climate change contingencies in conservation strategy. *Trends in Ecology & Evolution* **28**:135–142.
- Graham CH, VanDerWal J, Phillips SJ, Moritz C, Williams SE. 2010. Dynamic refugia and species persistence: tracking spatial shifts in habitat through time. *Ecography* **33**:1062–1069.
- Hall ND. 2008. The centennial of the Boundary Waters Treaty: a century of United States-Canadian transboundary water management. *Wayne Law Review* **54**:1417.
- Hamann A, Aitken SN. 2013. Conservation planning under climate change: accounting for adaptive potential and migration capacity in species distribution models. *Diversity and Distributions* **19**:268–280.
- Hampe A, Rodriguez-Sanchez F, Dobrowski S, Hu FS, Gavin DG. 2013. Climate refugia: from the Last Glacial Maximum to the twenty-first century. *New Phytologist* **197**:16–18.
- Hannah L. 2011. Climate change, connectivity, and conservation success. *Conservation Biology* **25**:1139–1142.
- Hannah L, Midgley G, Anelma S, Araujo M, Hughes G, Martinez-Meyer E, Pearson R, Williams P. 2007. Protected area needs in a changing climate. *Frontiers in Ecology and the Environment* **5**:131–138.
- Hargreaves AL, Eckert CG. 2014. Evolution of dispersal and mating systems along geographic gradients: implications for shifting ranges. *Functional Ecology* **28**:5–21.
- Heller NE, Zavaleta ES. 2009. Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biological Conservation* **142**:14–32.
- Hiley JR, Bradbury RB, Holling M, Thomas CD. 2013. Protected areas act as establishment centres for species colonizing the UK. *Proceedings of the Royal Society B-Biological Sciences* **280**:20122310.
- Hill J, Collingham Y, Thomas C, Blakeley D, Fox R, Moss D, Huntley B. 2001. Impacts of landscape structure on butterfly range expansion. *Ecology Letters* **4**:313–321.
- Hill JK, Griffiths HM, Thomas CD. 2011. Climate change and evolutionary adaptations at species' range margins. Pages 143–159 in Berenbaum MR, Carde RT, Robinson GE, editors. *Annual Review of Entomology*. Volume **56**. Annual Reviews, Palo Alto, CA.
- Hobday AJ. 2011. Sliding baselines and shuffling species: implications of climate change for marine conservation. *Marine Ecology* **32**:22.
- Hoegh-Guldberg O, Hughes L, McIntyre S, Lindenmayer DB, Parmesan C, Possingham HP, Thomas CD. 2008. Assisted colonization and rapid climate change. *Science* **321**:345–346.
- Hoffmann AA, Sgro CM. 2011. Climate change and evolutionary adaptation. *Nature* **470**:479–485.
- IPCC. 2013. Climate change 2013: the physical science basis. Working Group I contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM, editors. Cambridge University Press, Cambridge, United Kingdom.
- Janin A, Lena JP, Ray N, Delacourt C, Allemand P, Joly P. 2009. Assessing landscape connectivity with calibrated cost-distance modelling: predicting common toad distribution in a context of spreading agriculture. *Journal of Applied Ecology* **46**:833–841.

- Johnston A, et al. 2013. Observed and predicted effects of climate change on species abundance in protected areas. *Nature Climate Change* **3**:1055–1061.
- Jurickova L, Horackova J, Lozek V. 2014. Direct evidence of central European forest refugia during the last glacial period based on mollusc fossils. *Quaternary Research* **82**:222–228.
- Keppel G, Van Niel KP, Wardell-Johnson GW, Yates CJ, Byrne M, Mucina L, Schut AGT, Hopper SD, Franklin SE. 2012. Refugia: identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography* **21**:393–404.
- Kerr JT, Kharouba HM, Currie DJ. 2007. The macroecological contribution to global change solutions. *Science* **316**:1581–1584.
- Kerr JT, Dobrowski SZ. 2013. Predicting the impacts of global change on species, communities and ecosystems: it takes time. *Global Ecology and Biogeography* **22**:3.
- Kharouba HM, Algar AC, Kerr JT. 2009. Historically calibrated predictions of butterfly species' range shift using global change as a pseudo-experiment. *Ecology* **90**:2213–2222.
- Kharouba HM, Kerr JT. 2010. Just passing through: Global change and the conservation of biodiversity in protected areas. *Biological Conservation* **143**:1094–1101.
- Kharouba HM, Paquette SR, Kerr JT, Vellend M. 2014. Predicting the sensitivity of butterfly phenology to temperature over the past century. *Global Change Biology* **20**:504–514.
- Kujala H, Araujo M, Thuiller W, Cabeza M. 2011. Misleading results from conventional gap analysis – Messages from the warming north. *Biological Conservation* **144**:9.
- Kujala H, Burgman MA, Moilanen A. 2013a. Treatment of uncertainty in conservation under climate change. *Conservation Letters* **6**:73–85.
- Kujala H, Moilanen A, Araujo MB, Cabeza M. 2013b. Conservation planning with uncertain climate change projections. *PLOS ONE* **8** (e53315) DOI:10.1371/journal.pone.0053315.
- Lawler JJ. 2009. Climate change adaptation strategies for resource management and conservation planning. *Annals of the New York Academy of Sciences* **1162**:79–98.
- Lawson CR, Bennie JJ, Thomas CD, Hodgson JA, Wilson RJ. 2012. Local and landscape management of an expanding range margin under climate change. *Journal of Applied Ecology* **49**:552–561.
- Lemieux CJ, Beechey TJ, Gray PA. 2011. Prospects for Canada's protected areas in an era of rapid climate change. *Land Use Policy* **28**:928–941.
- Lenormand T. 2002. Gene flow and the limits to natural selection. *Trends in Ecology & Evolution* **17**:183–189.
- Leroux SJ, Larrivee M, Boucher-Lalonde V, Hurford A, Zuloaga J, Kerr JT, Lutscher F. 2013. Mechanistic models for the spatial spread of species under climate change. *Ecological Applications* **23**: 815–828.
- Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD. 2009. The velocity of climate change. *Nature* **462**:1052–1055.
- Loss SR, Terwilliger LA, Peterson AC. 2011. Assisted colonization: Integrating conservation strategies in the face of climate change. *Biological Conservation* **144**:92–100.
- Loyola RD, Lemes P, Nabout JC, Trindade J, Sagnori MD, Dobrovolski R, Diniz JAF. 2013. A straightforward conceptual approach for evaluating spatial conservation priorities under climate change. *Biodiversity and Conservation* **22**:483–495.
- Maclean IMD, Wilson RJ. 2011. Recent ecological responses to climate change support predictions of high extinction risk. *Proceedings of the National Academy of Sciences of the United States of America* **108**:12337–12342.
- Mawdsley J. 2011. Design of conservation strategies for climate adaptation. *Wiley Interdisciplinary Reviews-Climate Change* **2**:498–515.
- McMahon SM, Harrison SP, Armbruster WS, Bartlein PJ, Beale CM, Edwards ME, Kattge J, Midgley G, Morin X, Prentice IC. 2011. Improving assessment and modelling of climate change impacts on global terrestrial biodiversity. *Trends in Ecology & Evolution* **26**:249–259.
- Moritz C, Agudo R. 2013. The future of species under climate change: Resilience or decline? *Science* **341**:5.
- Munoz MM, Stimola MA, Algar AC, Conover A, Rodriguez AJ, Landestoy MA, Bakken GS, Losos JB. 2014. Evolutionary stasis and lability in thermal physiology in a group of tropical lizards. *Proceedings of the Royal Society B-Biological Sciences* **281**:9.
- Newman JA. 2011. *Climate Change Biology*. CABI, Wallingford, United Kingdom.
- Norberg J, Urban MC, Vellend M, Klausmeier CA, Loeuille N. 2012. Eco-evolutionary responses of biodiversity to climate change. *Nature Climate Change* **2**:747–751.
- Ockinger E, Bergman KO, Franzen M, Kadlec T, Krauss J, Kuussaari M, Poyry J, Smith HG, Steffan-Dewenter I, Bommarco R. 2012. The landscape matrix modifies the effect of habitat fragmentation in grassland butterflies. *Landscape Ecology* **27**:121–131.
- Pearson RG, Dawson TP. 2005. Long-distance plant dispersal and habitat fragmentation: identifying conservation targets for spatial landscape planning under climate change. *Biological Conservation* **123**:13.
- Popescu VD, Patrick DA, Hunter ML, Calhoun AJK. 2012. The role of forest harvesting and subsequent vegetative regrowth in determining patterns of amphibian habitat use. *Forest Ecology and Management* **270**:163–174.
- Pyke CR, Anelman SJ, Midgley G. 2005. Identifying priority areas for bioclimatic representation under climate change: a case study for Proteaceae in the Cape Floristic Region, South Africa. *Biological Conservation* **125**:9.
- Raimer F, Ford T. 2005. Yellowstone to Yukon (Y2Y) - one of the largest international wildlife corridors. *Gaia-Ecological Perspectives for Science and Society* **14**:182–185.
- Reside AE, et al. 2013. Climate change refugia for terrestrial biodiversity: Defining areas that promote species persistence and ecosystem resilience in the face of global climate change. *National Climate Change Adaptation Research Facility, Gold Coast, Australia*.
- Reusch TBH, Wood TE. 2007. Molecular ecology of global change. *Molecular Ecology* **16**:3973–3992.
- Rist L, Campbell BM, Frost P. 2013. Adaptive management: Where are we now? *Environmental Conservation* **40**:5–18.
- Rose N-A, Burton PJ. 2009. Using bioclimatic envelopes to identify temporal corridors in support of conservation planning in a changing climate. *Forest Ecology and Management* **258**:5:11.
- Rose N-A, Burton PJ. 2011. Persistent climate corridors: The identification of climate refugia in British Columbia's Central Interior for the selection of candidate areas for conservation. *BC Journal of Ecosystems and Management* **12**:101–117.
- Sackett LC, Cross TB, Jones RT, Johnson WC, Ballare K, Ray C, Collinge SK, Martin AP. 2012. Connectivity of prairie dog colonies in an altered landscape: inferences from analysis of microsatellite DNA variation. *Conservation Genetics* **13**:407–418.
- Sanderson EW, Jaiteh M, Levy MA, Redford KH, Wannebo AV, Woolmer G. 2002. The human footprint and the last of the wild. *BioScience* **52**:891–904.
- Sauer JR, Fallon JE, Johnson R. 2003. Use of North American Breeding Bird Survey data to estimate population change for bird conservation regions. *Journal of Wildlife Management* **67**:372–389.
- Sauer JR, Link WA, Fallon JE, Pardieck KL, Ziolkowski Jr DJ. 2013. The North American breeding bird survey 1966–2011: summary analysis and species accounts. *North American Fauna* **79**:1–32.
- Sax DF, Early R, Bellemare J. 2013. Niche syndromes, species extinction risks, and management under climate change. *Trends in Ecology & Evolution* **28**:517–523.
- Sgro CM, Lowe AJ, Hoffmann AA. 2011. Building evolutionary resilience for conserving biodiversity under climate change. *Evolutionary Applications* **4**:326–337.

- Shoo L, Hoffmann A, Garnett S, Pressey R, Williams Y, Taylor M, Falconi L, Yates C, Scott J, Alagador D, et al. 2013. Making decisions to conserve species under climate change. *Climatic Change* **119**:239–246.
- Skelly DK, Freidenburg LK. 2010. Evolutionary responses to climate change. eLS. DOI: 10.1002/9780470015902.a0022545.
- Soons MB, Heil GW. 2002. Reduced colonization capacity in fragmented populations of wind-dispersed grassland forbs. *Journal of Ecology* **90**:1033–1043.
- Stefanescu C, Carnicer J, Penuelas J. 2011. Determinants of species richness in generalist and specialist Mediterranean butterflies: the negative synergistic forces of climate and habitat change. *Ecography* **34**:353–363.
- Stephenson B. 2001. The Algonquin to Adirondack conservation initiative: a key macro-landscape linkage in eastern North America. George Wright Society, Hancock, MI.
- Svenning JC, Normand S, Kageyama M. 2008. Glacial refugia of temperate trees in Europe: insights from species distribution modelling. *Journal of Ecology* **96**:1117–1127.
- Torok P, Vida E, Deak B, Lengyel S, Tothmeresz B. 2011. Grassland restoration on former croplands in Europe: an assessment of applicability of techniques and costs. *Biodiversity and Conservation* **20**:2311–2332.
- Travis MJ. 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society B-Biological Sciences* **270**:467–473.
- Tremblay MA, St Clair CC. 2011. Permeability of a heterogeneous urban landscape to the movements of forest songbirds. *Journal of Applied Ecology* **48**:679–688.
- Vié J-C, Hilton-Taylor C, Stuart SN. 2009. *Wildlife in a changing world: an analysis of the 2008 IUCN Red List of threatened species*. IUCN, Gland, Switzerland.
- Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, Roy DB, Telfer MG, Jeffcoate S, Harding P, et al. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* **414**:65–69.
- Webber BL, Scott JK. 2012. Rapid global change: implications for defining natives and aliens. *Global Ecology and Biogeography* **21**:305–311.
- Weeks AR, Sgro CM, Young AG, Frankham R, Mitchell NJ, Miller KA, Byrne M, Coates DJ, Eldridge MD, Sunnucks P. 2011. Assessing the benefits and risks of translocations in changing environments: a genetic perspective. *Evolutionary Applications* **4**:709–725.
- White PJT, Kerr JT. 2007. Human impacts on environment-diversity relationships: evidence for biotic homogenization from butterfly species richness patterns. *Global Ecology and Biogeography* **16**:290–299.
- Williams JW, Jackson ST. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* **5**:475–482.
- Williams JW, Jackson ST, Kutzbach JE. 2007. Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences of the United States of America* **104**:5738–5742.
- Williams JW, Kharouba HM, Veloz S, Vellend M, McLachlan J, Liu Z, Otto-Bliesner B, He F. 2013. The ice age ecologist: testing methods for reserve prioritization during the last global warming. *Global Ecology and Biogeography* **22**:13.