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Source: Natural Areas Journal, 36(4):440-452.
Published By: Natural Areas Association
DOI: http://dx.doi.org/10.3375/043.036.0410
URL: http://www.bioone.org/doi/full/10.3375/043.036.0410

Dispersal Limitation, Climate Change, and Practical Tools for Butterfly Conservation in Intensively Used Landscapes

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Natural Areas Journal 36:440–452

ABSTRACT: Pollinators, such as butterflies, contribute to vital ecosystem services, but are susceptible to changing thermal regimes associated with recent climate change. While butterflies are responding to climate changes in many ways, they are not keeping pace. Rapid climate changes are leading to an accumulation of climate debts (or loss of climatic habitat) at continental scales. Climate change mediated shifts in distribution depend on many factors, but particularly on species-specific dispersal abilities and availability of larval host plants. We measured geographical variation in mobility for butterfly species across North America relative to their conservation status and the intensity of human land use. We identified areas where the rate and variability of recent climatic changes have been relatively low and could be managed for pollinator conservation, potentially augmenting existing protected area networks. Using the Yellowstone to Yukon region as a case study, we outline differences between connectivity analyses that incorporate (i) human footprint, (ii) human footprint in conjunction with climate change considerations, and (iii) human footprint in conjunction with climate change considerations weighted by species mobility and richness. All three approaches yield different connectivity recommendations. Conservation management efforts to enhance climate change-related dispersal should focus on improving landscape connectivity based on species-specific mobility, richness, and climate change, as well as landscape permeability. Improving connectivity is particularly vital in areas where mobility and landscape permeability are low but species are at greatest risk of extinction. Mobility matters when considering efforts to mitigate climate change impacts on butterflies.

Index terms: butterflies, climate change, connectivity, ecological services, host plant interactions

INTRODUCTION

Habitat loss and climate change alter species distributions (Warren et al. 2001; Breed et al. 2013) and increase extinction rates (Wake and Vredenburg 2008; Barnosky et al. 2011; Estes et al. 2011). Biodiversity loss, in turn, alters ecosystem function. Recent assessments indicate that such changes may soon be irreversible (Rockstrom et al. 2009; Steffen et al. 2015). Climate changes have been sufficiently rapid that even highly mobile pollinators often cannot track shifting conditions quickly enough to avoid accumulating climate debts (namely a loss of climatic space that can leave species in areas of decreasing suitability; Devictor et al. 2012). Pollinator species have been lost across southern regions of both Europe and North America during recent climate change (Devictor et al. 2012; Kerr et al. 2015a). Declines in some species can directly affect ecosystem functions and services, such as pollination (Tylianakis et al. 2008; Potts et al. 2010). Changes in pollination services have the potential to alter ecological communities (Biesmeijer et al. 2006; Bloch et al. 2006). Butterflies contribute to the stability and resilience of ecosystems (Kruess and Tscharntke 2002) through pollination of wildflowers during nectaring (Wallis DeVries et al. 2012; Martins 2014). Many non-bee insects, such as Lepidopterans, have additional practical benefit as pollinators for global cropping systems (Rader et al. 2016).

Temperature strongly affects butterfly population dynamics (Breed et al. 2013), and recent climate changes have strongly affected butterfly communities (Menendez et al. 2006; Devictor et al. 2012; Breed et al. 2013). Critical life history events such as pupation, larval emergence, and overwintering, and processes such as mobility (which affects dispersal and population dynamics), are mediated by specific physiological requirements that are influenced by weather (McLaughlin et al. 2002; Cormont et al. 2011; Williams et al. 2012). Basking and use of microclimates reduce exposure to thermal stress and promote essential functions, such as resource acquisition or seeking mates (Barton et al. 2014). However, behavioral thermoregulation provides only partial relief from temperature extremes and cannot compensate for sustained shifts in temperature that exceed organismal tolerances over long periods (Kingsolver et al. 2011; Radchuk et al. 2013).

Geographical range shifts are a common response to climate change (Oliver et al. 2015). Yet, habitat losses and fragmentation reduce the likelihood that species can disperse to new areas (Fernández-Chacón et al. 2014). Species with poor dispersal capabilities have higher risks of climate change related extinction (Urban et al. 2012), but certain species' traits can mitigate susceptibility to negative effects of climate change (Kotiaho et al. 2005; Öckinger et al. 2010). For instance, habitat and host plant specialists (Warren et al. 2001) may have difficulty dispersing through matrix areas that fail to meet specialized requirements, leading to increased susceptibility to land use change among such species (Singer and Parmesan 2010; Winfree et al. 2011). Moreover, species in decline are less likely to track shifting climatic conditions (Mair et al. 2014). Enhancing landscape connectivity could improve dispersal prospects for species with limited mobility (Oliver et al. 2015), although such enhancements may take different forms, depending on species' dispersal capacities (Robillard et al. 2015).

Butterfly physiology is temperature-dependent (Franke et al. 2014; Kingsolver and Buckley 2015), meaning that changing temperature regimes represent a strong selective force (Breed et al. 2013). Distinguishing between phenotypic plasticity and evolutionary responses can be challenging, but it is clear that phenotypic responses to changing climates can unfold quickly. For instance, larger wing area is linked to improved dispersal ability through reduced wing loading and energy demand during flight (Sekar 2012; Stevens et al. 2012). Because of the strong link between butterfly metabolic rate and temperature, warming temperatures alter energy consumption and potential allocation of resources to foraging and growth. *Boloria chariclea* (Schneider) and *Colias hecla* (Lefebvre) adults, observed continuously between 1996 and 2013, have declined in size with warming in northeastern Greenland, likely because of increased larval metabolic rates (Hanski et al. 2006). With declining wing sizes, these species' dispersal capacities may have declined also, with potential costs for reproductive output (Hanski et al. 2006).

While many responses to climate change are possible, in general, species with greater mobility (Ducatez et al. 2014) are more likely to keep pace with rapidly shifting climate conditions, particularly in regions with greater landscape connectivity (Hill et al. 2002; Oliver et al. 2015). Realized mobility—the capacity of species to colonize new areas despite barriers that may be present—needs to be assessed and integrated into conservation and management decision making. Based on a preexisting butterfly mobility database for North America (Burke et al. 2011), we present an assessment of spatial variation in butterfly mobility. Using a gap analysis and connectivity assessment, we demonstrate how this information can be used as a novel approach to regional connectivity planning. Climate and landuse changes are two of the key conservation threats confronting pollinator species, such as butterflies. Both threats can be mitigated when mobility and connectivity are high. Our approach integrates anticipated climate change impacts, as well as species-specific mobility, into more typical regional conservation planning considerations (such as size, adjacency, and representativeness of protected areas). We identify a range of conservation management options that address climate change related dispersal requirements within fragmented landscapes and which can be used to account for differences in mobility. The objective is to improve prospects for regional strategies that manage and conserve species and ecosystems (Scott et al. 1993), while accounting for factors such as landscape heterogeneity (Perović et al. 2015) and subregional differences in the variability and rate of climate change.

METHODS

Study Area

For assessments of butterfly species mobility and conservation status, we focused on continental North America north of Mexico. Watershed boundaries from the Commission on Environmental Cooperation (2010) were used to define conservation management priorities for species climate change related dispersal and distribution shift requirements in fragmented landscapes. We additionally define state-level conservation management priorities for the continental United States (Appendices A and B). We have not measured such priorities for Canadian provinces and territories because they are generally far larger than individual US states.

Captions below for Figures 1, 2, and 3, which are shown on the following page.

Figure 1. Mean mobility by watershed for butterfly species assemblages across North America. Map is based on 170 species for which geographical distributions and trait data were available. Mobility estimates draw on expert lepidopterists' opinions (see Burke et al. 2011). Mobility is an index of the capacity of butterfly species to disperse to new localities, potentially reflecting a rate-limiting step in the process of geographical range shifts that are necessary for many species to track shifting climatic conditions.

Figure 2. Mean conservation status by watershed for the 170 North American butterfly species for which mobility estimates were available. Inset map of conservation status for the most imperiled species in a watershed.

Figure 3. Areas of high butterfly diversity, intensive human influence (measured as "footprint"), and the distribution of both formal protected areas and zones where the rate and variability of climate change ("climate vulnerability") are low. While the region retains extensive wilderness, encroachment from development could limit future range shifts for pollinators unless key areas are prioritized for connectivity and reduction of fragmentation threats. Butterfly species richness is highest within the northern USA and southern Canada; climate change mediated dispersal will involve poleward range expansion. Intensive human influence east of Jasper and Banff National Parks will hinder broad scale connectivity efforts but could be targeted locally. A large area of low climate vulnerability (teal) to the north of the Peace River site (northeast of Graham-Laurier Provincial Park Regions and southeast of Northern Rocky Mountains Park) could provide much needed connectivity for species moving through landscapes between Yellowstone and Yukon. Smaller areas of low climate vulnerability occur throughout the Peace River site, to the northwest. Species in this region have intermediate or poor dispersal capacities (e.g., Figure 1), and are more likely to require conservation intervention to avoid accumulating biologically significant climate debts. All data are in Lambert Conformal Conic projection.

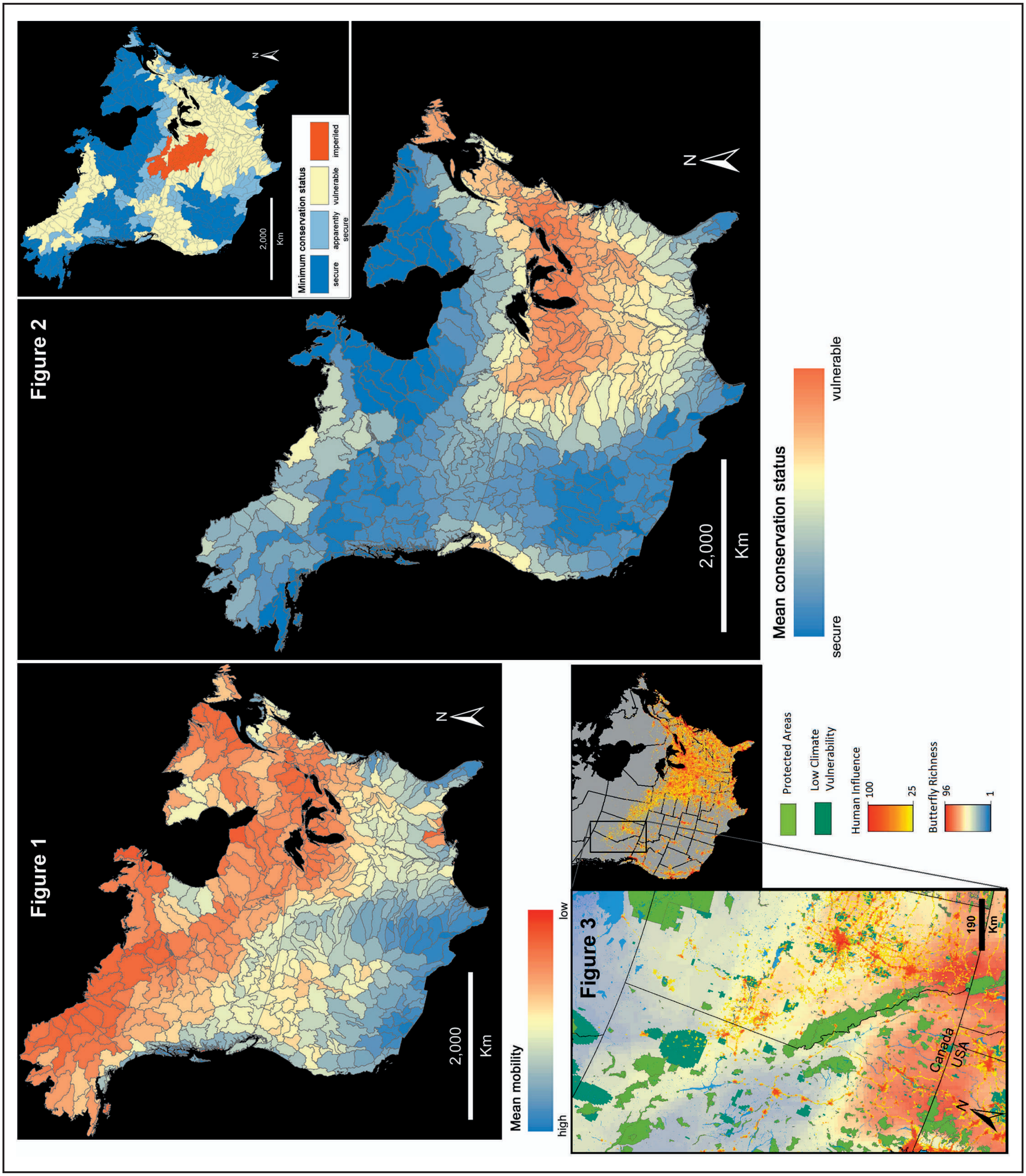
Figure 1
N
2,000
Km
Mean mobility
high
low
Figure 2
N
2,000
Km
Mean conservation status
secure
vulnerable
Minimum conservation status
secure
apparently secure
vulnerable
imperiled
Figure 3
Protected Areas
Low Climate Vulnerability
Human Influence
100
25
Butterfly Richness
96
1
190
Km
Canada
USA
N

Butterfly Species Occurrence Data

We assessed butterfly species richness at 5-arc minute resolution (approximately 10 km) for 170 North American butterflies (Refer to BioOne for Appendix C). Species were selected on the basis of data availability for range maps (Scott 1986), conservation threat status (NatureServe 2015), and mobility (expert Lepidopteran estimates on a scale between 1 and 10, see Burke et al. 2011). Mobility, an index of relative dispersal capacity, for the species included in this study range between 2.6 (sedentary species with weak capacities to disperse to new locations to establish populations) and 8.6 (highly mobile species that colonize new areas readily). We constructed a spatial metric of butterfly community mobility for all 170 species based on average mobility for species within watersheds. To our knowledge, this represents the first spatial representation of butterfly community mobility at a continental extent (Figure 1). Under changing climatic conditions, improved mobility is expected to relate to improved dispersal through fragmented landscapes undergoing climate changes. Management intensities and practices can be tailored to mobility in order to achieve conservation objectives.

We calculated the mean and greatest global conservation status (from least to most secure, categories were: 1 – critically imperilled, 2 – imperilled, 3 – vulnerable, 4 – apparently secure, and 5 – secure) for all butterfly species by watershed (NatureServe 2015). While mean conservation status for the species assemblages provides an indication of overall priority for management, greatest conservation status (i.e., the most serious level of threat among species in a watershed; Figure 2) can inform the immediacy of interventions (Kuussaari et al. 2009).

Regional Case Study

To underscore how species' mobility can interact with risks posed by climate change, we generated a gap analysis of existing protected areas and landuse intensity relative to assemblage level species mobility estimates and recent (1975–2010) climate changes, within a subset of the North American study region. We used this information to generate least cost path connectivity recommendations using the LinkageMapper software (McRae and Kavanagh 2011). The case study region centers on a section of the Rocky Mountains that lies within the Yellowstone to Yukon corridor and extends from the northern United States protected areas of Glacier National Park and the Bob Marshall Wilderness Area, into Canada along Banff National Park, Jasper National Park, and the Northern Rocky Mountains Park (Figure 3).

Climate Change Vulnerability

We assessed spatial variation in exposure to climate change-induced risks by measuring the rate and variability in climatic conditions between 1975 and 2010 using high resolution (5 arc-minute) climatic information. The North American climate surface was derived from gridded interpolated weather station observations (for details, see Hutchinson 2004; McKenney et al. 2011; Xu and Hutchinson 2013). We measured six aspects of climate that are likely to be relevant to butterfly or host plant persistence including mean, minimum, and maximum annual temperatures, precipitation in the wettest quarter, precipitation in the driest quarter, and precipitation seasonality. Using these climate variables, we generated a relative assessment of how rapidly climate has changed, and how variable climate is becoming, for every pixel covering terrestrial North America relative to a moving window extending outward from that pixel at nine spatial scales ranging from 50- to 450-km diameter (Coristine et al. unpub. data). Regions where the rate and variability of climate change are lower than in surrounding areas are analogous to climatic refugia observed during past glacial periods. We identified regions that preserved (i) lower rate and reduced variability, or (ii) higher rate and increased variability of climate change for any one of these bioclimatic variables at any spatial scale. These regions were assigned (respectively) as less vulnerable or more vulnerable to climate change.

Landuse Intensity Data

Protected areas data for both the United States and Canada were obtained from the World Database on Protected Areas (2015). We retained International Union for the Conservation of Nature protected area categories: Ia – strict nature reserve, Ib – wilderness area, II – national park, III – natural monuments, IV – species management areas, V – protected landscape or seascape, and VI – protected area with managed use of natural resources. Land classified as either permanently or temporarily unassigned was excluded. Although information on conservation easements, private land acquisitions, and municipal parks would further inform this analysis, such data were not readily available at international scales and were omitted. Regional planning should incorporate all available data for protected areas, including the boundaries of privately-managed conservation areas and landcover, which can inform planning for species-specific habitat requirements and connectivity. Human footprint data is based on level of fragmentation arising from population density, urbanization, transportation and electrical infrastructure, as well as landcover and landuse (Wildlife Conservation Society 2005). Areas with the most intensive human impacts are likely to pose steeper barriers to dispersal for many species (Warren et al. 2001; Öckinger et al. 2012).

Connectivity Analysis

We generated least-cost path connectivity analyses based on three different datasets that differ in landscape resistance to dispersal using the Linkage Mapper software (McRae and Kavanagh 2011). The first connectivity analysis used human footprint (Wildlife Conservation Society 2005) as a resistance layer, with increased levels of human landuse and infrastructure associated with higher resistance. The second analysis added climate change vulnerability (categorized as high, moderate, or low). Regions with high climate change vulnerability were set as the maximum resistance (i.e., 100) so that connectivity would be minimized in these areas. Regions with low or attenuated climate change were used to down-weight human footprint by 25%, while moderate values represent the standard expectation under climate change and did not alter resistance calculations. The third connectivity analysis combined the dispersal limiting effects of human footprint and climate change by assigning conservation priority based on relative species richness and sedentariness (i.e., inverse mobility score). All resistance layers were scaled between 1 and 100. Within the study area, we included protected areas larger than 4000 km^2 and identified corridors for the three nearest neighbours using Linkage Mapper tool in ArcGIS 10.0 (McRae and Kavanagh 2011; ESRI 2014). We assessed total corridor length, corridor overlap with already established protected areas (>4000 km^2), and overlap between corridors generated under differing resistance scenarios.

RESULTS

Across North America, average butterfly mobility shows substantial spatial variation and ranges between 3.3 and 7.6 (5.72 + 0.28) on a relative scale. Butterfly assemblages in southern regions show greater average mobility (Figure 1). A disproportionate number of butterfly species in eastern North America are vulnerable to extinction (Figure 2). The most imperilled butterfly species in North America tend to be found in regions where the mean conservation outlook for butterfly species is generally poor (Figure 2 inset).

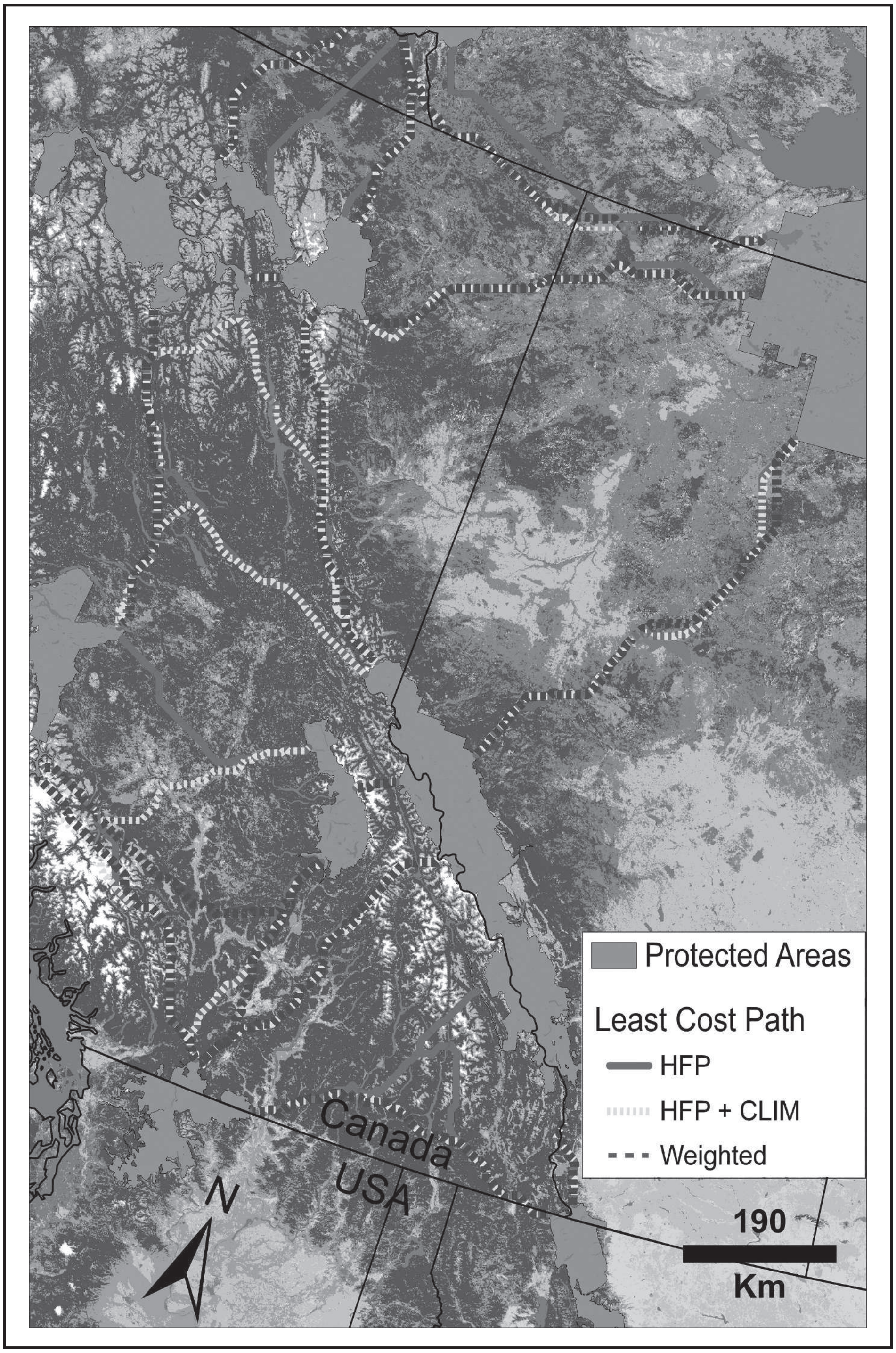

Figure 4. Least cost path configurations between twelve protected areas (> 4000 km^2) within the case study region. Connectivity assessments are based on three different resistance scenarios that incorporate elements of human footprint, climate change, species richness, and species' mobility. The map background shows land cover data at 250-m resolution (CEC 2005). All data are in Lambert Conformal Conic projection.

Human footprint and landuses, climate change rate and variability, as well as species richness and species mobility (Figure 3) all exhibit pronounced spatial variation across the study region. Least cost path (LCP) corridors provide dramatically different recommendations depending on which factors are considered (i. human footprint, ii. human footprint and climate change rate/variability, iii. human footprint and climate change rate/variability weighted by species richness and mobility). A least cost path weighted by relative species mobility and species richness as well as climate change rate and variability identifies different regions from either human footprint (x^2 = 5.1, p = 0.02) or human footprint and climate change (x^2 = 20.3, p = 6.7 x 10^{-6}) LCPs. However, a comparison of nonoverlap for LCPs between human footprint versus human footprint with climate change were similar (x^2 = 1.6, p = 0.2). Formally protected areas comprise a very low proportion of LCPs for any scenario (Figure 4, Table 1).

Table 1. Least cost path parameters for three different resistance layers within the study region.

Resistance Layer	Total Length of LCP (km)	Total Park Distance (km)	Cost Weighted Distance to Path Length	Cost Weighted Distance to Euclidean Distance
Human Footprint	5114	360	3.01 ± 0.98	3.84 ± 1.21
Human Footprint + Climate Change	5326	306	3.62 ± 1.15	4.64 ± 1.37
Human Footprint + Climate Change weighted by assemblage level sedentariness	4684	315	2.55 ± 0.40	3.27 ± 0.55

DISCUSSION

Pollinators that are less mobile face greater extinction risk (Burke et al. 2011; Urban et al. 2012). To the extent that species' distributions reflect climatic constraints, climate change will require species to disperse to new locations (Coristine and Kerr 2015). The rate at which species disperse needs to be at least equal to the rate at which areas of suitable climate shift for species to avoid climate debt and elevated extinction risk (Leroux et al. 2013). Yet, species' intrinsic dispersal abilities vary considerably across regions. Maintenance or restoration of landscape connectivity, or more intensive interventions like managed relocation (Kerr et al. 2015b; Robillard et al. 2015), take on greater urgency in areas where species are more sedentary, as in northern portions of North America (Figure 1). Species-specific (or fine-filter) interventions are likely to remain an essential complement to efforts that consider landscape connectivity relative to geographical variation in species' traits (Goddard et al. 2010). While scientific evidence, like anticipated changes in biotic communities (Schweiger et al. 2012), obviously informs conservation decisions (Sutherland et al. 2004), increased consideration of geographical variation in trait-based, individual species' dispersal capacities represents a constructive addition to conservation management.

Existing management practices that are designed to sustain local pollinator populations can improve landscape connectivity. Promoting positive pollinator response is possible through both local and regional conservation management. Establishing and maintaining pollinator-friendly gardens by creating breeding and nectaring habitat (Pywell et al. 2011), and facilitating behavioral thermoregulation and overwintering survival by maintaining habitat heterogeneity and structure (Ashton et al. 2009; Franke et al. 2014), benefit conservation for species already present in particular landscapes. However, such efforts may also increase landscape permeability, particularly in areas where butterfly assemblages are less mobile (Box A). Prevalence of butterflies with either relatively poor dispersal capacities, or poor conservation outlook, in prairie regions and in some high intensity agricultural landscapes in eastern North America (Figures 1, 2) suggests where pollinator management activities will be most valuable. Other management and restoration activities, like managed burns in prairie and savannah habitats (Vogel et al. 2007), or managed relocation for host plants along the leading edges of their distribution (Table 2), can similarly improve conservation prospects for pollinators in general and butterflies in particular. Monitoring programs and citizen science initiatives, such as eButterfly.org (Larrivee et al. 2014) or BumblebeeWatch.org can provide rapid feedback on how species are responding to particular conservation activities, as well as improving and sustaining public engagement and education.

Connectivity Planning in an Era of Climate Change

Connectivity planning that improves protection or management of areas with valuable habitat characteristics for butterfly species (and other pollinators) while integrating areas with lower climate change vulnerability and lower human footprint will mitigate extinction risk for species regardless of their individual conservation statuses (Brook 2008; Iwamura et al. 2013; Eigenbrod et al. 2015; Figure 4, Table 1). The intent for such actions is to increase the likelihood that species already present in an area will be conserved as climate changes, and to improve the likelihood of successful colonization of the area by new species arriving in the region because of changing climatic conditions (Kharouba and Kerr 2010), thus maximizing the efficiency of conservation efforts. A shift towards interjurisdictional conservation management strategies, as well as data sharing, will facilitate climate change specific interventions (Wolkovich et al. 2012; Camacho and Beard 2014).

While butterfly species are responding rapidly to climate change in comparison with other taxa (Walther et al. 2002; Chen et al. 2011), even butterfly species frequently fail to track climate change rapidly enough to avoid incurring climate debts (Bedford et al. 2012; Devictor et al. 2012). Activities that improve landscape connectivity, in order to increase the likelihood that species' dispersal rates will keep pace with shifting climatic conditions, should include at least four key considerations. First, recognize areas where species assemblages' least commonly have sufficient, intrinsic capacities to disperse to new areas (e.g., Figure 1). Second, when selecting areas with potential value as corridors, include consideration of the rate and variability of recent climate change, focusing particularly on areas where those measurements are lowest (e.g., Figures 3, 4). Third, manage landscapes for heterogeneity for behavioural thermoregulation (Kleckova et al. 2014) and provide diverse host plant resources (Hanspach et al. 2014). Finally, facilitate species dispersal by leveraging local efforts, like pollinator gardening or habitat management (e.g., burns), that improve landscape permeability for specialists or species of conservation concern (Dennis

BOX A: Wildwood Butterfly Garden by the Upper Thames River Conservation Authority

Management of natural areas for pollinator conservation can have far reaching impacts if conducted so as to enhance community education and outreach while integrating efforts with other initiatives. The Wildwood Butterfly Garden, located in southwestern Ontario (Canada), was initiated by the Upper Thames River Conservation Authority in 2015. The Wildwood Butterfly Garden occupies 600 m^2 and created butterfly and bee pollinator habitat on previously mown lawn. The garden's conservation benefits take different forms:

(1) The garden includes considerations for both butterflies in general, as well as species of conservation concern. Notably, requirements of monarch butterflies were specifically included in the design. Monarch butterflies have undergone drastic population declines over the past decade (Brower *et al.* 2012; Pleasants & Oberhauser 2013) mainly due to loss of their larval host-plant throughout the breeding range (Flockhart *et al.* 2015). Milkweed, the larval food source for monarch butterflies, was an important component of the garden and enables the site to be designated as a Monarch Waystation through the Monarch Watch Program.

(2) Through community education and outreach, the Wildwood Garden engaged 75 participants in efforts to increase nectaring and larval habitat in order to reduce habitat fragmentation and climate change threats for native butterfly species.

(3) The garden builds on an existing education and outreach program designed for school-age children, and is a complement to a previous butterfly garden and Monarch Waystation at the nearby Fanshawe Conservation Area, as well as ongoing wildflower plantings through the conservation authority's Communities for Nature Program.

Butterfly gardens increase landscape permeability and improve between-patch colonization for butterflies (Fernández-Chacón *et al.* 2014). Benefits of butterfly conservation efforts can be enhanced even further through anticipation of leading edge distribution shift, which requires consideration of rates of species-specific poleward dispersal for both butterflies and their nectaring and larval host-plants. These issues can be particularly important for species that are of conservation concern. The selection of host and nectaring plants for the Wildwood Butterfly Garden included consideration of shifting distributions. Local conservation management initiatives, such as butterfly gardens, can benefit existing and anticipated pollinator communities.

Brower, L.P., Taylor, O.R., Williams, E.H., Slayback, D.A., Zubieta, R.R. & Ramirez, M.I. (2012) Decline of monarch butterflies overwintering in Mexico: is the migratory phenomenon at risk? *Insect Conservation and Diversity,* **5,** 95-100.

Fernández-Chacón, A., Stefanescu, C., Genovart, M., Nichols, J.D., Hines, J.E., Paramo, F., Turco, M. & Oro, D. (2014) Determinants of extinction-colonization dynamics in Mediterranean butterflies: the role of landscape, climate and local habitat features. *Journal of Animal Ecology,* **83,** 276-285.

Flockhart, D., Pichancourt, J.B., Norris, D.R. & Martin, T.G. (2015) Unravelling the annual cycle in a migratory animal: breeding-season habitat loss drives population declines of monarch butterflies. *Journal of Animal Ecology,* **84,** 155-165.

Pleasants, J.M. & Oberhauser, K.S. (2013) Milkweed loss in agricultural fields because of herbicide use: effect on the monarch butterfly population. *Insect Conservation and Diversity,* **6,** 135-144.

Box A.

Table 2. Heuristic depiction of conservation management actions intended to benefit pollinators. Trade-offs between spatial scale of impact and intensity of effort (in terms of financial resources, personnel, effort, etc.) can identify optimal management strategies, but should be considered relative to anticipated changes in species distributions as well as net ecological benefit. Actions with potential to generate networks are likely to have greater conservation benefits (see Box A).

INTENSITY OF EFFORT (time, money, personnel, etc.): Low → High

SPATIAL SCALE OF IMPACT: Low → High

Intensity of effort	Spatial scale of impact: Low	Spatial scale of impact: High
High	• Butterfly corridor on land periphery • Vertical/thermal structuring of habitat	• Restoration (i.e. prairie burn) • Facilitated colonization of host plants for butterflies at their leading edge • Management of existing natural areas
Low	• Encourage landowner participation in government and private land conservation programs • Education and outreach • Create stepping stone habitat (i.e. butterfly gardens)	• Systematic monitoring (i.e. butterfly checklist (inclusive of southern species that may be expanding ranges), eButterfly – citizen science) • Community or roadside habitat plantings

et al. 2013; see Box A, Table 2, Refer to BioOne for Appendix C).

Improving Species Dispersal

Initiatives to enhance connectivity involve trade-offs between the scale at which effects will be realized, and the intensity of effort required, whether in terms of financial or personnel resources (Table 2). Improved biodiversity outcomes are possible by managing for connectivity among natural areas across a range of spatial extents (Beier et al. 2011), such as landscape permeability considered from the perspective of individual species (i.e., host plant interactions, see Menz et al. 2011), habitat availability and connectivity to account for regional ecosystem processes (i.e., topographical and vegetative structure that promotes ecosystem integrity and biodiversity in general; Tambosi et al. 2014), and landscape planning and prioritization at national or continental extents (i.e., establishment of new areas of greatest conservation value). The benefits of maintenance or restoration of local connectivity within a regional framework are significant. These activities maintain or create microhabitats or microclimates (Kleckova et al. 2014), augment resource availability (Dennis and Hardy 2007), and can be scaled up from localities to networks across landscapes. Management activities need to account for anticipated environmental conditions, such as increasing likelihood of summer droughts or spring floods, not just contemporary conditions.

CONCLUSION

Dialogue between landuse managers and researchers improves the likelihood that both relevant research goals and conservation successes can be achieved (Laurance et al. 2012). Increased data accessibility, available in formats suited to landuse management and conservation (Figures 1, 3), further supports beneficial conservation outcomes. Many of the tools and techniques outlined herein can be generalized to other taxa and may be particularly suitable for landowner engagement and involvement. For instance, tools such as citizen science programs can detect differences in biotic communities quickly and engage public interest in conservation outcomes.

Landscapes need to be managed by recognizing future, as well as current, climate change impacts. Some areas may require intensive management to avoid loss of species because of substantial regional variation in the capacity of species to respond geographically to changing climatic conditions. Other areas may require anticipation of, and planning for, peripheral populations. Regions with lower rates of climate change reduce the likelihood that species or populations are exposed to weather extremes, thereby increasing population abundance (Roland and Matter 2013) and poleward colonization (Crozier 2004). In the main, natural areas connectivity requires recognition that many species are dispersal-limited, even in the absence of intensive land uses. Areas with more threatened and specialist species (Refer to BioOne for Appendix C) will likely require greater and more sustained conservation effort.

ACKNOWLEDGMENTS

Laura Coristine dedicates her portion of this manuscript to two extraordinary individuals who understand the importance of building both community and community engagement - Helen Patterson and Bob Vandenberg. Jeremy Kerr is grateful for NSERC Discovery Grant support, funds through his University of Ottawa Research Chair in Macroecology and Conservation, and infrastructure from the Canadian Foundation for Innovation and Ontario Ministry of Research and Innovation. All data, including butterfly species mobility estimates, are available on request from the authors.

Laura Coristine recently completed her PhD at the University of Ottawa. She is a current Liber Ero Fellow at the University of Calgary. Her research focuses on conservation management strategies that reduce climate change impacts on Canada's biodiversity. She is currently working on conceptual advances that apply climate change research to landscape connectivity efforts, at macroecological scales. Her work involves multijurisdictional collaboration with conservation practitioners and decision-makers.

Peter Soroye is a master's student at the University of Ottawa. He is interested in science policy and in improving tools for researchers and practitioners to enable more effective biodiversity conservation. His work to date has focused on evaluating citizen science as a research tool, using eButterfly as a model system. His past endeavours include work examining indirect genetic effects in fungi and analyzing past climate and vegetation of the Ottawa area.

Rosana Nobre Soares is a master's student at the University of Ottawa. She is interested in biodiversity conservation and studying interacting effects of extinction drivers on broad-scale biodiversity patterns. Her current research focuses on the influence of local landscape factors on broad-scale distributional patterns of butterfly species. Her work emphasizes the importance of landscape-level adaptations to facilitate climate change induced range shifts across heavily human modified landscapes.

Cassandra Robillard is an Environmental Professional In-Training (EPt) and an MSc graduate in Biology and Sustainability from the University of Ottawa. Her Master's research focused on the efficient prioritization of areas for habitat restoration and conservation at a national scale, particularly within farmland.

Jeremy Kerr is Professor of Biology and holds the University Research Chair in Macroecology and Conservation at the University of Ottawa. His pure and applied research program focuses on understanding how environmental changes affect species and ecosystems and on how to improve prospects for conservation. He focuses particularly on butterflies and bumblebees. Kerr's work has been featured in media around the world and in Parliamentary briefings and presentations in the United Kingdom and Canada. He is President-elect of the Canadian Society for Ecology and Evolution (CSEE) and very active at the science-policy interface, contributing to development of national science and conservation policy and legislation in Canada. Kerr was elected to the Global Young Academy and is a member of the University of Ottawa's Institute for Science, Society, and Policy.

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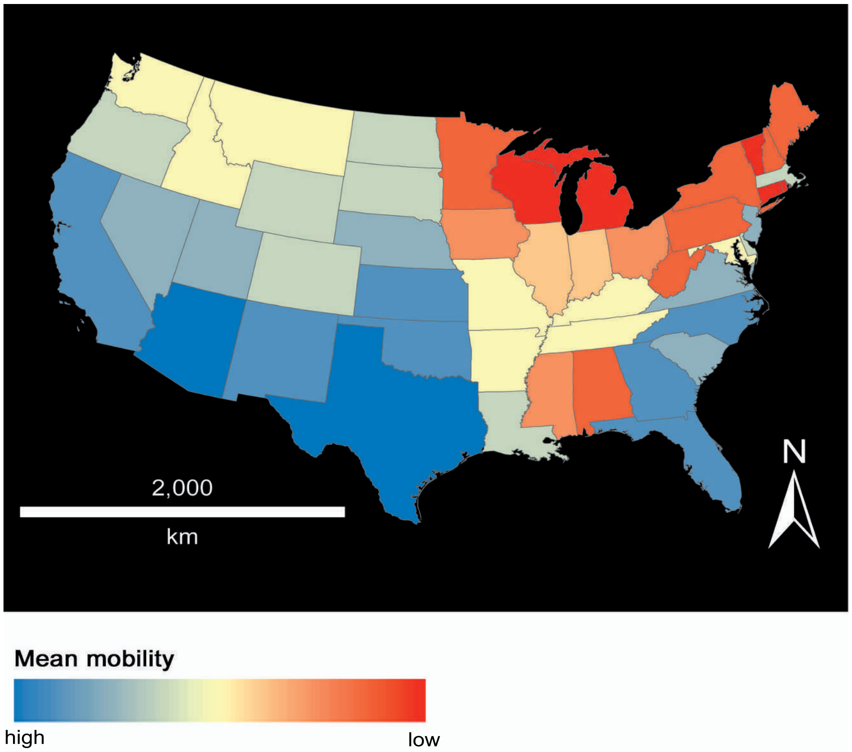
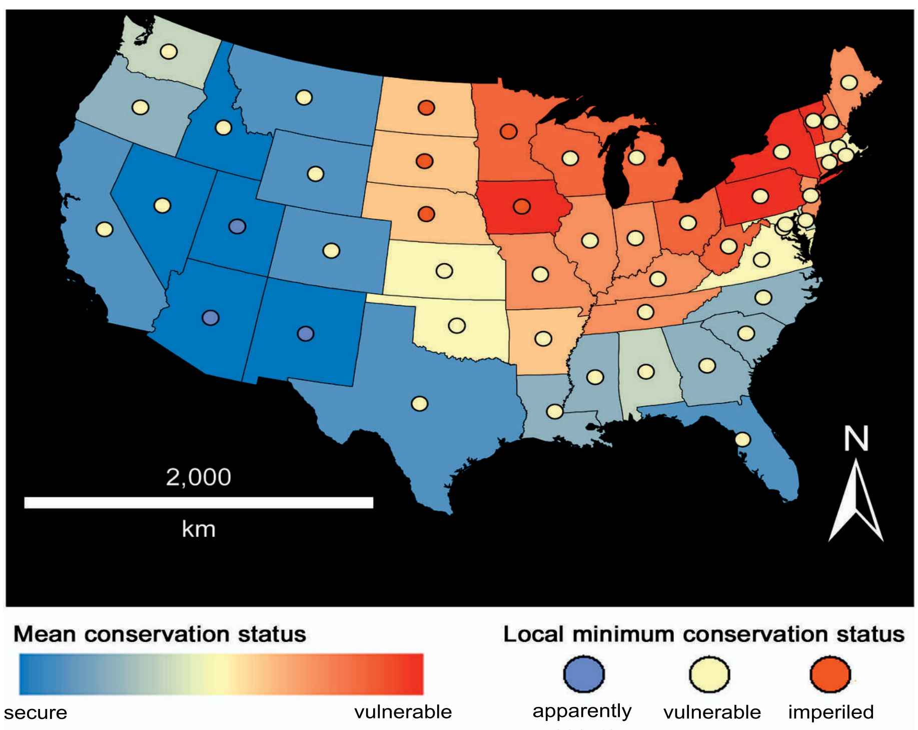


Appendix A. Mean mobility by state across the continental United States for butterfly species assemblages across North America. Map is based on 170 species for which geographical distributions and trait data were available. Mobility estimates draw on expert lepidopterists' opinions (see Burke et al. 2011).



Appendix B. Mean conservation status by state across the continental United States for the 170 North American butterfly species for which mobility estimates were available. Solid colors represent mean mobility while circular data points denote conservation status for the most imperiled species in a state.

Appendix C. Refer to BioOne for list of 170 butterfly species and the associated conservation status, mobility estimate, and larval host breadth.