Landscape permeability improves climate-based predictions of butterfly species persistence

by

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"In the end we will conserve only what we love; we will love only what we understand; and we will understand only what we have been taught."

― Baba Dioum

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Abstract:

Habitat modification alters species' capacities to track shifting climatic conditions. Broad-scale analyses that explore demographical responses to on-going climate change tend to neglect the influence of the underlying landscape pattern. However, many landscapes are fragmented by human activities, which might make dispersal for many species more challenging. Determining the extent to which landscape factors affect broad-scale distributional patterns has implications for our ability to predict realistic climate change impacts on species. Here, we constructed species-specific measurements of landscape permeability for 96 butterfly species in southern Ontario to test whether this landscape characteristic affected species' distributions at macroecological scales. We used multiple logistic regression models to test for the effects of permeability and its interaction with temperature on butterfly species presence/absence. We found that 48% of butterfly species responded to landscape permeability alone or in interaction with temperature. In general, the effect was positive (87%) and species were more likely to be present with increasing landscape permeability. For 61% of the species that responded to broad-scale landscape permeability, the interaction of temperature with permeability was statistically significant. In warm areas, species were more likely to be present if landscape permeability was high. Landscape permeability explained 3-43% of residual variability in species' presences after accounting for temperature. Finally, we show how fine-scale permeability measurements can be combined with large-scale patterns of diversity to inform conservation efforts. Landscape permeability can affect species' distributions at broad-scales and understanding factors that potentially influence species' dispersal can improve predictions for how species respond to changing climatic conditions.

Résumé

La modification des habitats change la capacité des espèces à suivre les conditions climatiques changeantes. Les analyses à grande échelle qui explorent les réponses démographiques aux changements climatiques ont tendance à négliger l'influence de la structure du paysage sous-jacent. Cependant, de nombreux paysages sont fragmentés par les activités humaines, ce qui pourrait rendre la dispersion de nombreuses espèces plus difficiles. La détermination de quel point les facteurs de paysage affectent les modes de distribution géographiques des espèces à grande échelle a des répercussions sur notre capacité à prédire les impacts réalistes des changements climatiques sur les espèces. Dans cette thèse, nous avons construit des mesures spécifiques de la perméabilité du paysage pour chaque des 96 espèces de papillons dans le sud de l'Ontario pour vérifier si cette caractéristique du paysage affecte la distribution géographiques des espèces à grandes échelles spatiales. Nous avons utilisé les modèles de régression logistique pour évaluer les effets de la perméabilité du paysage et son interaction avec la température sur la présence et absence des espèces de papillons. Nous avons trouvé que 48% des espèces de papillons ont répondu seulement à la perméabilité du paysage ou en interaction avec la température. En général, l'effet était positif (87%) et les espèces étaient plus susceptibles d'être présentes avec l'augmentation de la perméabilité du paysage. Pour 61% des espèces qui ont répondu à la perméabilité du paysage à grande échelle spatiale, l'interaction de la température avec la perméabilité était statistiquement significative. Dans les régions chaudes, les espèces étaient plus susceptibles d'être présentes si la perméabilité du paysage était élevée. La perméabilité du paysage a expliqué 3-43% de la variabilité résiduelle des présences des espèces en tenant compte de la température. Enfin, nous avons montré comment les mesures de perméabilité à l’échelle fine peuvent être combinées avec des modèles

de la diversité des espèces à grande échelle pour informer les efforts de conservation. La perméabilité du paysage peut affecter les distributions des espèces à a grande échelle et la compréhension des facteurs qui peuvent influencer la dispersion des espèces peut améliorer les prévisions des façons dont les espèces répondent aux conditions climatiques changeantes.

Introduction

Global change is accelerating extinction rates substantially (Barnosky et al. 2011, Lancaster 2016). Habitat destruction and climate change are the main forces driving this global loss of biodiversity (Travis 2003). Often the impacts of these anthropogenic stressors on species are studied and managed in isolation (Mantyka-pringle et al. 2012, Titeux et al. 2016). However, these global change drivers will act simultaneously and their interaction could accelerate the dynamics of extinction (Harte et al. 2004, Opdam and Wascher 2004, Pyke 2004, Thomas et al. 2004, Thuiller et al. 2004, Brook et al. 2008, Titeux et al. 2016). Conservation strategies are more likely to be effective as mechanisms to protect global biodiversity if they mitigate the effects of co-occurring drivers of extinction (Oliver and Morecroft 2014, Titeux et al. 2016).

Determining which environmental factors shape species' distributions will help predict their responses to environmental change. However, underlying processes that drive distributional patterns vary with grain size and geographical extent (Luoto et al. 2007, Xu et al. 2014). This scale dependency leads to differences in the use of environmental determinants to model species distributions at varying spatial scales. Macroecological studies often assess biodiversity patterns at coarse grains and large geographical extents (Beck et al. 2012, Martins et al. 2014, Xu et al. 2014, Valdés et al. 2015) and focus primarily on determinants over broad-scales (i.e. climate) as the main drivers of those broad-scales patterns (Parmesan et al. 2005, Luoto et al. 2007, Jansson 2009, Yamaura et al. 2009, Reino et al. 2013). On the other hand, landscape-scale studies are conducted at smaller grain sizes and spatial scales (Xu et al. 2014), where finer-scale factors such as habitat availability and connectivity are important determinants of species distribution (Luoto et al. 2007, Reino et al. 2013, Fernández-Chacón et al. 2014, Xu et al. 2014). The strength of the relationship between climatic factors and diversity patterns (e.g. richness) becomes stronger as grain size increases, whereas the strength of the relationship between landscape attributes and those same patterns become weaker at larger grain sizes (Luoto et al. 2007). Determining and utilizing the optimal resolution (large spatial extent with small spatial grain) to assess the effects of climatic and landscape attributes in conjunction can be challenging but necessary since factors operating at different spatial scales, from landscapes (e.g. habitat availability and fragmentation) to regions (e.g. climate), could interact to affect species geographical ranges (Heffernan et al. 2014) .

The effects of habitat loss and fragmentation on species' distributions have been widely studied (Debinski and Holt 2000, Fahrig 2003, Fischer and Lindenmayer 2007, Reino et al. 2013, Fernández-Chacón et al. 2014, Haddad et al. 2015). Fragmentation is the conversion of natural habitat to human land uses, which alters the spatial configuration of remaining suitable habitat and the composition of the surrounding matrix (Thomas 2000, H. Ricketts 2001, Opdam and Wascher 2004, Bailey 2007, Haddad et al. 2015). The distance between the remaining suitable habitat and the matrix that surrounds them, determines the extent to which the permeability of the landscape impedes species dispersal. Species' dispersal capacities vary considerably (Leroux et al. 2013, Robillard et al. 2015), as do their habitat preferences, leading to the need to develop species-specific landscape metrics. At local scales, landscape structure plays a key role in colonization-extinction dynamics by modifying the costs and benefits of dispersal (Thomas 2000, Bonte et al. 2012, Delattre et al. 2013). In fragmented landscapes, dispersal rates are lower and mortality rates are higher (Thomas 2000, Schtickzelle et al. 2006, Sweaney et al. 2014). Landscape permeability predicts colonization rates for most butterfly species (38 of 53) within monitoring sites in Catalonia and the Balearic Islands (Fernández-Chacón et al. 2014).

Thermal conditions strongly influence population dynamics and activity patterns (e.g. foraging time) for ectotherms (White and Kerr 2007, Gunderson and Leal 2016). For butterfly species, temperature has been shown to be a main determinant of species ranges (Kharouba et al. 2009). Habitat fragmentation alters thermal conditions in remnant habitat patches and leads to hotter, drier, more variable microclimate conditions compared to regions with continuous habitat (Laurance 2004). In fragmented landscapes, resources are spatially isolated and successful movement among such habitat is a prerequisite for butterfly species survival (Davis et al. 2007). Habitat isolation disrupts butterfly activity by increasing the time spent in a matrix where mortality risks are higher, and by reducing the time spent on activities needed to survive (e.g. resource acquisition and reproduction) (Davis et al. 2007). Another challenge of dispersal in fragmented landscapes is that behavioural thermoregulation can be difficult in the matrix surrounding suitable habitat which leads to increased thermal stress (Sunday et al. 2014, Tuff et al. 2016). Pervasive habitat loss and fragmentation create barriers that may disrupt species' capacities to respond to other extinction stressors, such as rapidly shifting climatic conditions (Brook et al. 2008, Mantyka-pringle et al. 2012, Pimm et al. 2014).

Projected shifts in species geographical distributions relative to changes in climate have been extensively studied, but accounting for the influence of landscape pattern and species' potential dispersal rates has proven difficult, particularly because of limited availability of species-specific habitat requirements and dispersal capacities (Schloss et al. 2012, Travis et al. 2013). Because of the complexity of incorporating landscape metrics into broad-scale analysis, it is often assumed that habitat is continuous, which will permit a climate-driven geographical response that is only limited by a shift in temperature, not the landscape (Travis 2003). A meta-analysis that examined studies that focus on projected biodiversity scenarios under environmental change found that most studies took a single stressor approach with the majority of studies focusing only on climate as the driving force and only 10% of studies combined climate and land-use to develop biodiversity scenarios (Titeux et al. 2016). This dominant use of climate and neglect for landscape-related factors in projections of biodiversity scenarios has been increasing in the past 25 years (Titeux et al. 2016). However, the potential for species to adapt to climate change will depend largely on the ability of species to move across broad landscapes (McRae et al. 2012, Schloss et al. 2012). Therefore, focusing only on climate-driven responses may lead to inaccurate projections of species' distributions under climate change (Bakkenes et al. 2002, Travis 2003, Schloss et al. 2012, Bennie et al. 2013, Titeux et al. 2016).

The structure of the landscape could affect range occupancy towards climatically-determined range boundaries amongst butterfly species by altering dispersal rates and the likelihood that species can colonize isolated areas (Hanski et al. 1995, Thomas 2000, Hill et al. 2001, Schtickzelle et al. 2006, Wilson et al. 2009, Flick et al. 2012). Butterfly species' habitat requirements can vary across their ranges, becoming increasingly specialized toward range boundaries (Oliver et al. 2014, Pateman et al. 2016). Investigating the potential links between fine-scale local landscape processes and large-scale patterns may improve spatially explicit predictions of species responses to changes in environmental conditions and better inform biodiversity conservation efforts (Beck et al. 2012, Titeux et al. 2016).

The effects of habitat fragmentation on species' distributions are often examined at smaller spatial scales (i.e. patch scale to landscape scales). The extent to which these effects "scale up" to generate a signal over broader areas remains uncertain There is a growing need to address this knowledge gap and determine the extent to which landscape factors, which determine colonization success at local landscape scales (i.e. landscape permeability), affect broad-scale distributional patterns because restructuring of global biodiversity patterns, as a result of climate change induced range shifts, will be apparent and investigated at large spatial scales.

In this study, we bridged processes that operate at different spatial scales to determine the extent to which the effects of habitat fragmentation scale-up to influence large-scale distributions of butterfly species in heavily human-modified landscapes. We developed species-specific landscape permeability measurements that relate to each species' habitat preferences. We tested whether this landscape metric predicts butterfly species distributions over broad extents. Temperature is known to limit many butterfly species' distributions and to contribute to recently observed geographical range responses among these species to climate change, so we also tested whether landscape permeability interacts with climate to affect species' distributions across the study region. We expected a positive interaction between temperature and landscape permeability because species are more likely to colonize climatically suitable areas if landscape permeability is high. Finally, we used the results of these analyses to propose patterns of connectivity among protected areas across the study region to inform landscape-level strategies that attempt to mitigate the effects of climate change.

Methods

Study location and butterfly species' presence/absence

We focused on southern Ontario because it is a biodiversity hot spot for Canada and includes a range of land use pressures and pronounced climatic gradients (Coristine and Kerr 2011). Sampling intensity within this region is high, which permits measurement of butterfly species' distributions at a relatively fine grain size. Butterfly observations from 1960-2012 were collected from the Toronto Entomologist association, e-butterfly.org and Butterflies of Canada datasets (Layberry et al. 1998) and assembled into one large dataset. There were 157,195 georeferenced observations from this time period (Figure 1). The time period is long enough to enable reasonably large numbers of species observations and minimize sampling biases that may arise from changes in temporal and spatial sampling intensities. Long term observation datasets, like the one used in this study, are more likely to capture true absences (due to environmental conditions) within a species' range than range maps and therefore reflect species' spatial distributions more accurately (Hurlbert and Jetz 2007). We used a grid network of 25km x 25km to represent the distributions of butterfly species across southern Ontario. Conservation decision-making and land-use management is often performed at grain sizes of 10-1000km^2 (Dale et al. 2000). Geographical data were processed in ArcGIS 10.0 (Esri 2011).

A total of 96 butterfly species was included in the analyses. We excluded species that were either very range-restricted (occupied only a few quadrats) or that were ubiquitous (were present in all or nearly all quadrats). We focused on species with detectable range limits somewhere within the study region of southern Ontario and constructed models predicting their distributions using quadrats falling within those range limits. Four butterfly species' ranges included only southern areas of the study region (90 quadrats). Four butterfly species' ranges included only northern areas of the study region (174 quadrats), and the remaining 88 species' ranges included the entire study region (264 quadrats). To control for spatial variation in sampling intensity and minimize sampling bias, we determined the total number of butterfly species' observations per quadrat and included this measurement as a covariate in subsequent analyses.

Environmental variables

Climate

Monthly temperatures for the growing season (April-October) from 1960-2012 were obtained from Natural Resources Canada (5 arc-minute resolution; methods described in McKenney et al. 2011) and averaged for each grid cell (Appendix A). This measurement strongly relates to butterfly species' range limits in this region (Kharouba et al. 2009).

We used a land cover map (25m resolution) produced by the Ontario Ministry of Natural Resources (OMNR 2002) from Landsat Thematic Mapper (TM) scenes captured mainly in the 1990`s to determine which land covers were potentially suitable for each species' (see Appendix B for a table of suitable land cover types for each species). Species-specific habitat preferences were based on a broad cross-section of expert opinion (Layberry et al. 1998, Burke et al. 2011; and references therein). We then reclassified the land cover dataset based on species habitat preference with suitable habitat coded as 1 and unsuitable habitat coded as 0. This measurement of habitat suitability likely overestimates the availability of suitable areas for species because it relies on cover types rather than confirmed presences of suitable hostplants. Species richness was then measured by overlaying species binary ranges on the 25km x 25km grid system covering the study region.

Landscape structure

Our primary interest is on the ability of species to disperse across fragmented landscapes. Therefore, we used permeability to indicate the spatial variation of habitat fragmentation. Landscape permeability is a measure of landscape structure encompassing the connectedness of suitable habitat and the surrounding matrix of varying land uses. It is a direct measurement of the influence of landscape elements on dispersal (Koen et al. 2012, Schloss et al. 2012). To take into account the idiosyncratic responses of species to habitat fragmentation, we generated species-specific permeability metrics that: a) maps permeability as a continuous gradient (i.e. "cost" surface), b) enables a multi-species analysis and c) provides a spatially detailed measurement of areas where additional conservation efforts may be needed to improve landscape permeability.

We calculated a permeability index per pixel where the theoretical spread of a species from a focal pixel is a function of the "cost" of moving across that cell and the connectivity of that cell to the surrounding landscape (i.e. potential sources for dispersing individuals). We constructed (see Appenxic C for more information):

1) a generalized conductance surface layer (*Cond*) based on the land cover dataset, resampled to 100m (Koen et al. 2012, Graves et al. 2014),

2) a measurement of connectivity (*Conn*) using species-specific binary suitability maps, and,

3) a permeability map for each species (at 100m resolution) by combining conductance and connectivity and then extracting quadrat-level permeability measurements (Equation1),

$$\text{Pmi} = \sum\left(\frac{Cond\ X\ Conn}{N}\right)$$

(Equation1)

where Pmi is the average permeability index for the quadrat based on per-pixel measurements. We combined the 96 species-specific permeability maps in order to construct a generalized permeability estimate for these species for the study region, but we used species-specific measurements of permeability in models predicting butterfly distributions across the study region.

Finally, we used the generalized permeability map to illustrate strategies to establish protected or managed areas to facilitate species' movements across the region. The connectivity analysis used Linkage mapper to identify potential corridors between protected areas across southern Ontario. We obtained existing protected areas data for the study region (WDPA 2015) (Figure 2). We used the generalized permeability estimate as a resistance layer by taking its inverse and re-scaling it between 1-100, where increasing values indicate higher "cost" in terms of energy required for dispersal or mortality risks. We used protected areas as core regions to connect and generated least-cost path (Euclidean and cost-weighted distance) analysis based on this resistance layer by using Linkage Mapper in ArcGis 10.0 (McRae and Kavanagh, 2011).

Statistical analysis

All statistical analyses were performed in R, version 3.0.2 (R core team, 2013). We used multiple logistic regression analysis (glm, binomial family using a logit link function) to test for effects of permeability and its interaction with temperature on the probability of individual species' presence. Total number of observations was log-transformed and used as a covariate in all models to account for spatially varying sampling effort. When necessary, species-specific permeability measurements were similarly transformed to meet normality assumption. We standardized the continuous independent variables (by mean centering and dividing by the standard deviation) so that effects of variables within and among models could be compared directly (Schielzeth 2010). We fitted a full model, including the direct effects of permeability, temperature, the interaction of those variables, and observation numbers on probability of each species' presence (model1) as:

$$P_{(i)} = Obsv + T*Perm_{(i)}$$

where $P_{(i)}$ is probability the species i is present in a grid cell in the 1960-2012 period, Obsv is total number of observations, T is the mean temperature for the growing season, and $Perm_{(i)}$ is the species-specific permeability measurement. We evaluated the extent to which the inclusion of landscape permeability and its interaction with temperature improved predictions of presence/absence by computing the amount of variation explained by permeability. We calculated pseudo-R^2 (Nagelkerke, 1991) for models with statistically significant terms (based on model 1 calculations). We then removed permeability from these models and re-computed pseudo-R^2 using model 2:

$$P(i) \sim Obsv+T$$

We measured residual variation associated with permeability by taking the difference of the pseudo-R^2 from model 1 and the pseudo-R^2 from model 2 and then divided it by the unexplained variation from model1. Pseudo-R^2 for the models were computed using the

BaylorEdPsych package in R (R core team, 2013). We checked for evidence of multicollinearity between the independent variables by determining the variance inflation factor (VIF) for each regression coefficient.

Results

In total, 48% of butterfly species showed a direct or interactive effect (with temperature) of permeability (Appendix D, Table D1). The relative contribution of permeability to model predictions varied across species (Figure 7). Figures 4 and 5 shows the predictive accuracy for four butterfly species (Canadian tiger swallowtail, columbine duskywing, Henry's elfin and Eastern pine elfin) that had strong effects of permeability (pseudo-R^2 increased substantially when permeability was incorporated to purely species~climate models). The main effect of permeability was statistically significant (alpha=0.05) for 39 butterfly species (Figure 3). Species' presence was positively related to landscape permeability for 34 butterfly species. For five species (Black swallowtail, Eastern tiger swallowtail, Gray hairstreak, Appalachian brown and Giant swallowtail) the effect was negative, i.e these species' were less likely to be present in landscapes with high permeability. The interaction of temperature with permeability was statistically significant ($p<0.05$) for 24 butterfly species (Table 1.0). For 19 of 24 species, the effect was positive- the effect of temperature on the probability that a species would be present increased with increasing landscape permeability. In general, incorporating landscape permeability into the models improved model predictions. A paired t-test revealed that the pseudo-R^2 for the models with permeability was significantly higher (mean = 8.541, $p =<<<0.05$) than the pseudo-R^2 for the models without permeability (Figure 6). The amount of residual variation explained by incorporating permeability and its interaction with temperature varied across species (3%-43%) (Figure 7). There was no evidence of multicollinearity between the independent variables since the Vif values for the regression coefficients in the 46 models were all less than five (APPENDIX E Table E1).

Averaging the permeability measurements across all species (96 species) revealed a lot of spatial variation across the study region. Permeability in the southern region is much lower relative to further north (Figure 8). This permeability map was converted into a resistance layer to determine corridor recommendations between protected areas (Figure 9). A total of 185 protected areas (size ranged from 0.1012 km^2 to 7723km^2) was used as core areas to connect for the connectivity analysis. The majority of the protected areas (>70%) is concentrated further north (Figure 2). The southern most regions of the study area, which corresponds to where permeability is lower, only had 51 protected areas to connect and they tended to be relatively small (0.1012km^2 to 154km^2 , with a mean of 8.54km^2). We combined this fine-scale data with observed large-scale pattern of butterfly species richness to direct regional conservation effort in areas where it will be most valuable (Figure 10).

Discussion

We integrated fine-scale spatial variability of permeability with coarse-scale temperature to predict individual butterfly species distributions over a broad area. We hypothesized that landscape permeability, which was used as an indicator of local habitat fragmentation, would scale-up to influence large-scale distributional patterns of butterfly species. For the butterfly species that responded to landscape permeability, the general trend was positive- the probability of species' presence rose with increasing landscape permeability

(APPENDIX D, Table D1). We did find a negative effect of permeability on the probability of presence for five butterfly species- Black swallowtail, Eastern tiger swallowtail, Gray hairstreak, Appalachian brown and Giant swallowtail. Out of the five species, three are highly mobile swallowtails (black swallowtail, giant swallowtail and Eastern tiger swallowtail). This is an unexpected result because previous landscape-scale studies have found that highly mobile species are less affected by dispersal barriers and survive well in fragmented landscapes (Thomas 2000). A possible biological explanation for this significant negative relationship is that these highly mobile butterfly species are making dispersal decisions based on biotic interactions (i.e competition). Dispersal is riskier in areas where permeability is low and therefore may exclude many butterfly species. Highly mobile species, however, do not suffer dispersal limitations in these areas and can therefore exploit these regions with minimal competition. The addition of landscape permeability improved the predictive ability of broad-scale distribution models that included only climate. This finding suggests that the effect of decreased dispersal and colonization success observed in landscape-scale-studies of habitat fragmentation (Thomas 2000, Baguette et al. 2003, Schtickzelle et al. 2006, Fernández-Chacón et al. 2014) influences macroecological patterns and that failing to account for the spatial variation in species-specific landscape factors decreases the accuracy of predictions of species' distributions. This result is consistent with previous research that have examined the role of landscape factors in broad-scale patterns and found that land cover improved predictions for bird species distributions in Finland at 10-20km (Luoto et al. 2007), landscape fragmentation did influence large-scale distribution of a grassland specialist bird in the Iberian Peninsula (Reino et al. 2013) and local landscape attributes increased the explanatory power for broad-scale patterns of bird species richness in mainland China (Xu et al. 2014). Despite the importance of climate and habitat impacts on species' prospects for conservation, few studies have yet examined the influence of landscape structure and dispersal limitations on climate change-induced range shifts. Building on early research that focused on small geographical areas, single species, or simulation models (Hill et al. 2001, Travis 2003, Wilson et al. 2004), new research on larger species' assemblages over broad spatial and temporal scales could improve understanding of the processes that limit species' range responses to the combined effects of habitat fragmentation and climate change.

The interaction of landscape permeability with growing season temperature increased the likelihood of butterfly species' presences. Although detecting landscape structure effects at this scale is unexpected, several mechanisms could lead to these observations. Temperature influences the amount of time species remain active to acquire resources (White and Kerr 2006, Gunderson and Leal 2016). Consequently, warmer temperatures increase butterfly activity directly, but foraging and reproductive successes will be influenced by landscape structure. Habitat fragmentation makes dispersal to new areas riskier by requiring movement through potentially unsuitable habitats (Thomas 2000, Opdam and Wascher 2004, Wilson et al. 2009, Stefanescu et al. 2011, Fernández-Chacón et al. 2014). Thus, a permeable landscape is likely to increase the likelihood of a species reaching a new locality and successfully finding sufficient resources to maintain positive population growth once there. Therefore, species are more likely to be present where temperature is warm and the landscape is permeable because the environmental conditions are better for butterfly activity. Although this analysis was purely spatial, it does have implications for climate change research. Our results show that landscape permeability via an interaction with mean growing season temperature can affect the spatial distribution of butterfly species in regions where human pressure is high. As climate changes, thermal barriers that limit individual species' geographical range limits shift geographically, which results in shuffling of species ranges (Chen et al. 2011, Bedford et al. 2012). We expect that species' range responses to temperature change through time could mirror those we have observed spatially. If so, range responses should be more rapid in areas where landscape permeability is relatively high.

The results from this study have important implications for broad-scale conservation of biodiversity, particularly in the face of climate change. Extensive fragmentation of habitat degrades ecosystems, affects the long term persistence of species and is a major driver of global biodiversity decline (Haddad et al. 2015). Conservation planning, aimed at maintaining high butterfly diversity in areas where land use is intensive, should include strategies to increase permeability of surrounding landscapes on a broad spatial scale. Reducing the effects of habitat loss by protecting large tracts of continuous habitat and increasing the amount of natural habitat should still be the primary mechanism to protect biodiversity (Villard and Metzger 2014). However, in regions where land- uses are both intensive and extensive, these conservation initiatives may be unachievable over short time periods. For example, in the southernmost regions of Ontario, habitat loss is most pronounced. The primary cause of habitat loss within this region is conversion of habitat to agriculture (Coristine and Kerr 2011). Once natural habitat is converted to human land use, restoring habitat would be very costly and time consuming. Adapting and managing landscapes by increasing permeability may be a valuable conservation alternative to facilitate species’ range shifts and promote species’ persistence in regions where increasing habitat amount substantially is not a realistic conservation strategy.

Integrating landscape connectivity in conservation planning (e.g. protected areas design) and land-use management has become increasingly important, particularly in trans-national conservation challenges (McRae et al. 2012, Correa Ayram et al. 2015, Belote et al.

2016). Facilitating species' capacity to respond to warming climate through enhanced connectivity and permeability, can alter extinction patterns and promote the persistence of species in human-dominated landscapes. Here, we showed how broad- scale analysis of species-specific permeability measurements can be used as a tool to help identify large- scale dispersal networks to mitigate climate change impacts (McRae et al. 2012, Theobald et al. 2012). Our regional permeability assessment revealed that permeability tends to decrease further south of the study region (Figure 8), indicating that within this region, species may encounter more dispersal barriers making it harder to track climate change. The connectivity analysis also revealed that this is a region where protected areas are small and scarce (Figure 9). Conservation planners in this region should focus on both creating or growing existing protected area (perhaps through habitat restoration) and landscape level adaptations (i.e. butterfly gardens, corridors along agricultural fields) to facilitate climate change-related dispersal and promote long-term persistence of butterfly species. By combining the information from the least-cost path analysis with observed large-scale spatial variation of butterfly species richness, we can further inform conservation decisions by prioritizing corridors where richness is higher (Figure 10). This approach can easily be adapted for different species' groups or to meet particular conservation goals.

There are some limitations in our ability to explain butterfly species distributions at this geographical extent and spatial resolution. Models for several species explained only modest amounts of variation in species' presence/absence. Previous studies have suggested that butterfly species respond to landscape structure at the spatial extent of their daily movements, which is highly influenced by microclimatic variability (i.e. daily weather). Coarse environmental measurements here do not capture short-term, small scale environmental variability resulting in unexplained variation (Davis et al. 2007, Flick et al. 2012). The lack of knowledge of individual species' dispersal capabilities and the influence of various land cover types on species' dispersal limited our ability to construct species-specific permeability measurements. New field studies that focus on the effects of land use/cover on dispersal for large assemblage of species will be critical for understanding species spatial responses to environmental change. Imprecision of the land cover dataset could also be a factor that contributed to the high amounts of unexplained variation. The land cover dataset was used to construct species-specific binary suitability maps. The suitability maps represented a liberal measurement of habitat suitability because habitat preference was based on potentially suitable land covers, not on presence of host plants. Because it is unlikely that all potentially suitable land cover types represented actual suitable habitat (i.e. presence of host plants), this liberal measurement may fail to capture actual suitable habitat (i.e. presence of host plants) and may therefore be a poor indicator of availability of suitable habitat.

The spatial resolution of analysis can have an influence on inferences. Using a coarser spatial resolution (larger quadrats) to analyze species' spatial distribution patterns can lead to underestimation or masking of the effects of a given environmental variable. In order to minimize sampling bias, we had to increase the scale of the analysis by using larger than ideal quadrats. This may have underestimated or concealed the effect of landscape permeability on the assemblage of butterfly species in the study region. This could be in part why 52% of butterfly species did not show any response to landscape permeability at the scale of the analysis. The influence of grain size on inferences highlights the importance of the persistence of long term monitoring programs and citizen science initiatives, such as e-Butterfly.org, to increase the resolution within which we can measure species' responses to environmental determinants and obtain more reliable estimates. An increase in spatial and temporal data of butterfly species distributions would enable stronger tests of the effects observed in this study and determine if this spatial effect translates into effects through time.

To measure habitat fragmentation in this study required the scaling-up of high resolution (fine-grained) landscape permeability measurements. We were able to do this due to the availability of high resolution land cover data (25m) for Ontario, Canada. Some inaccuracies with the permeability measurements could arise due to mismatches between the land cover data and the longer-term collection period for butterfly observations because the land cover dataset was from a particular time period (the 90's -2002) and species observations covered a longer time period (1960-2012). High resolution land cover/use data across temporal scales and larger geographical extents (i.e. country wide) are usually unavailable, often leading to the use of coarser datasets (i.e. >1km) that may fail to capture fine-scale habitat fragmentation effects, such as permeability. Data limitations, such as the lack of small-grain, large-extent data for both species' distributions and environmental determinants, affect our ability to bridge the gap between landscape and macroecological scales in research and conservation. The integration of ecological processes that operate at different scales (from local to macro) is important if we want to accurately predict species' distributions and protect biodiversity in a time of rapid global change.

Conclusion

Landscape permeability can affect species' distributions at macroecological extents and understanding species' capacities to disperse through landscapes can enable better predictions of species' responses to global change. Habitat degradation and destruction is the primary driver of biodiversity decline. Neglecting landscape-related factors and focusing only on climate when developing projections of species distributions will lead to inaccurate representations of what biodiversity patterns will look like under environmental change. Further research on how multiple extinction drivers, such as climate change and habitat fragmentation, will interact across spatial and temporal scales to alter species geographical distributions, which will in turn alter biodiversity patterns, will be pivotal for designing and implementing effective conservation plans that will promote the persistence of species in the face of climate change.

Data limitations affect our ability to integrate processes that operate at different spatial scales. Here, we show an approach that can be used to integrate fine-scale data of processes that operate at local scales with coarse scale patterns of diversity to help inform conservation efforts over broad areas. Southern Ontario is a region of conservation concern because it is a biodiversity hotspot for Canada that coincides with intensive human land use pressure. The connectivity analysis revealed that to protect biodiversity within this study region, specifically the very south, land use management and conservation strategies that facilitate species' capacity to track shifting climatic condition through human imposed dispersal barriers is urgently needed. Conservation challenges we face today will require research that bridges the spatial scale gap between landscape ecology and macroecology. Increasing the availability of extensive, high resolution biodiversity datasets and their environmental determinants would provide a powerful tool to meet these future research needs.

Table 1: The logistic regression coefficient (log-odds) for the 24 butterfly species that had a significant interacting effect of permeability with climate.

Species (common name)	**Permeability* Temperature**
Common sootywing	1.8398**
White admiral	1.5176***
Mustard white	1.2006***
Arctic skipper	1.1598***
Harris' checkerspot	0.8622***
Henry's elfin	0.7704**
Canadian tiger swallowtail	0.7642**
Eastern pine elfin	0.7312**
Columbine duskywing	0.7123**
Silver-spotted skipper	0.703*
Gray comma	0.6849**
West virginia white	0.6587**
Northern pearly-eyes	0.629**
Silvery blue	0.5729**
Indian skipper	0.533**
Pink-edged sulphur	0.5326*
Gray hairstreak	0.511**
Leonard's skipper	0.4551*
Northern cloudywing	0.4446*
Acadian hairstreak	-0.388**
Bronze copper	-0.5876**
American lady	-0.7311**
Edward's hairstreak	-0.7439*
Silver checkerspot	-1.0611***

n=264

Significance codes: *** p < 0.001, ** p < 0.01, * p < 0.05

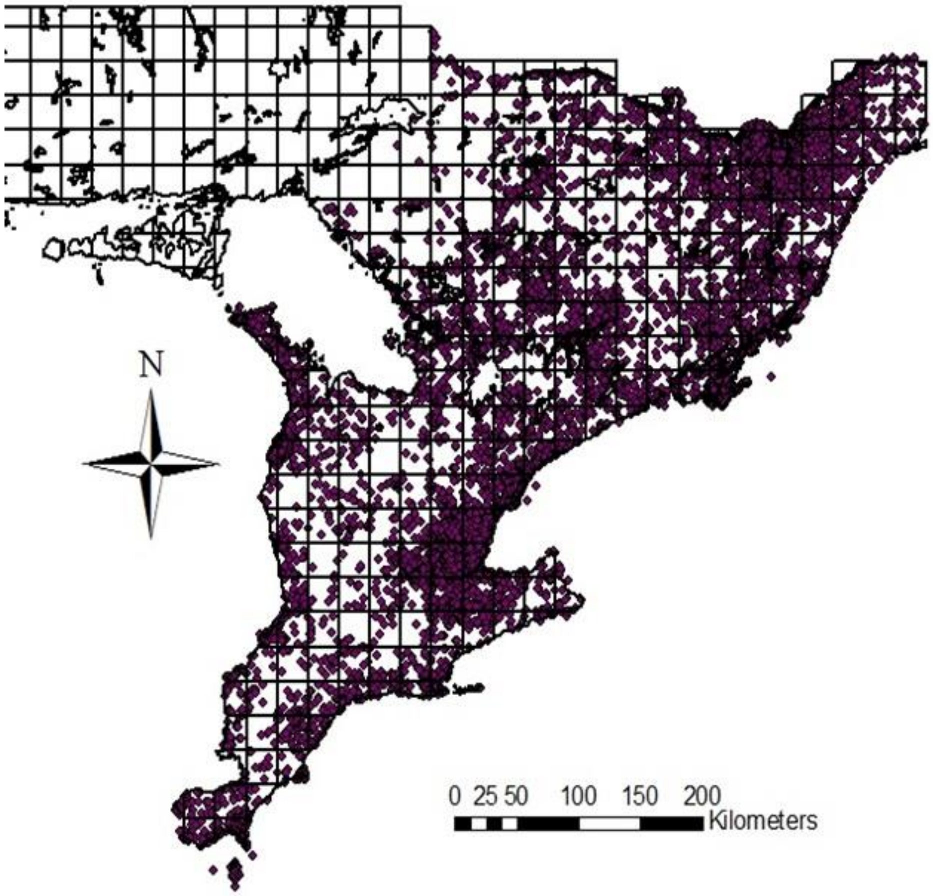

Figure 1: The study area is the southern part of Ontario. Quadrats are 25km x 25km and are outlined in black. Butterfly species observations across the study region are in purple (157,195 georeferenced observations).

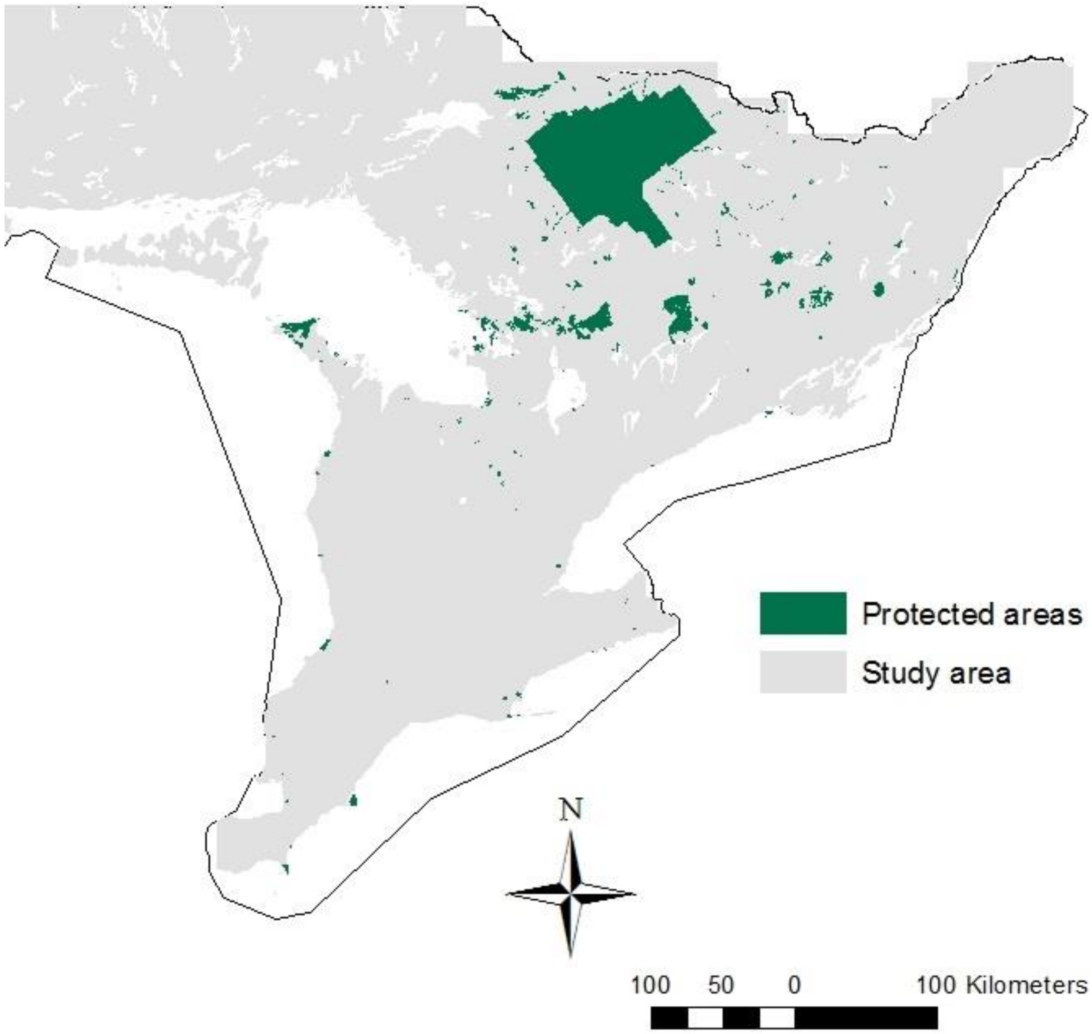

Figure 2: Protected areas throughout the study region. A total of 185 protected areas (size ranged from 0.1012 km^2 to 7723km^2) was used as core areas for subsequent connectivity analysis. Data are from the World database on protected areas (2015).

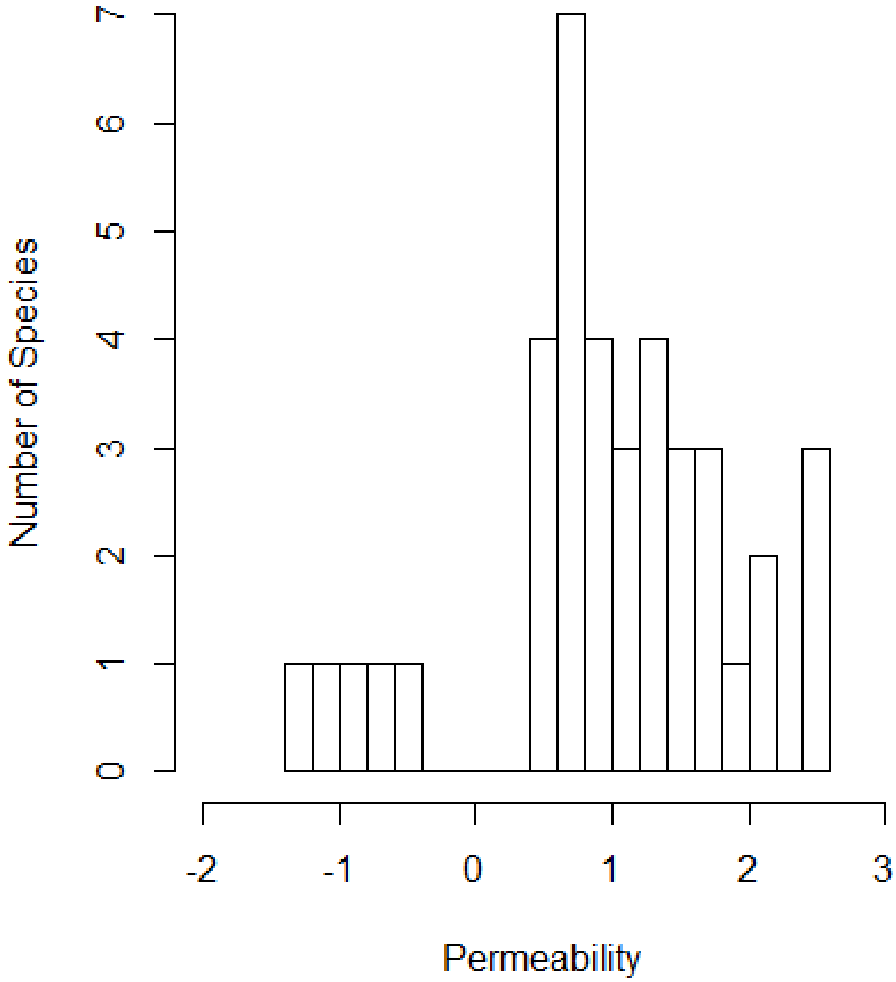

Figure 3: The distribution of the logistic regression coefficients (log odds)of permeability for the 39 butterfly species with a significant main effect of permeability.

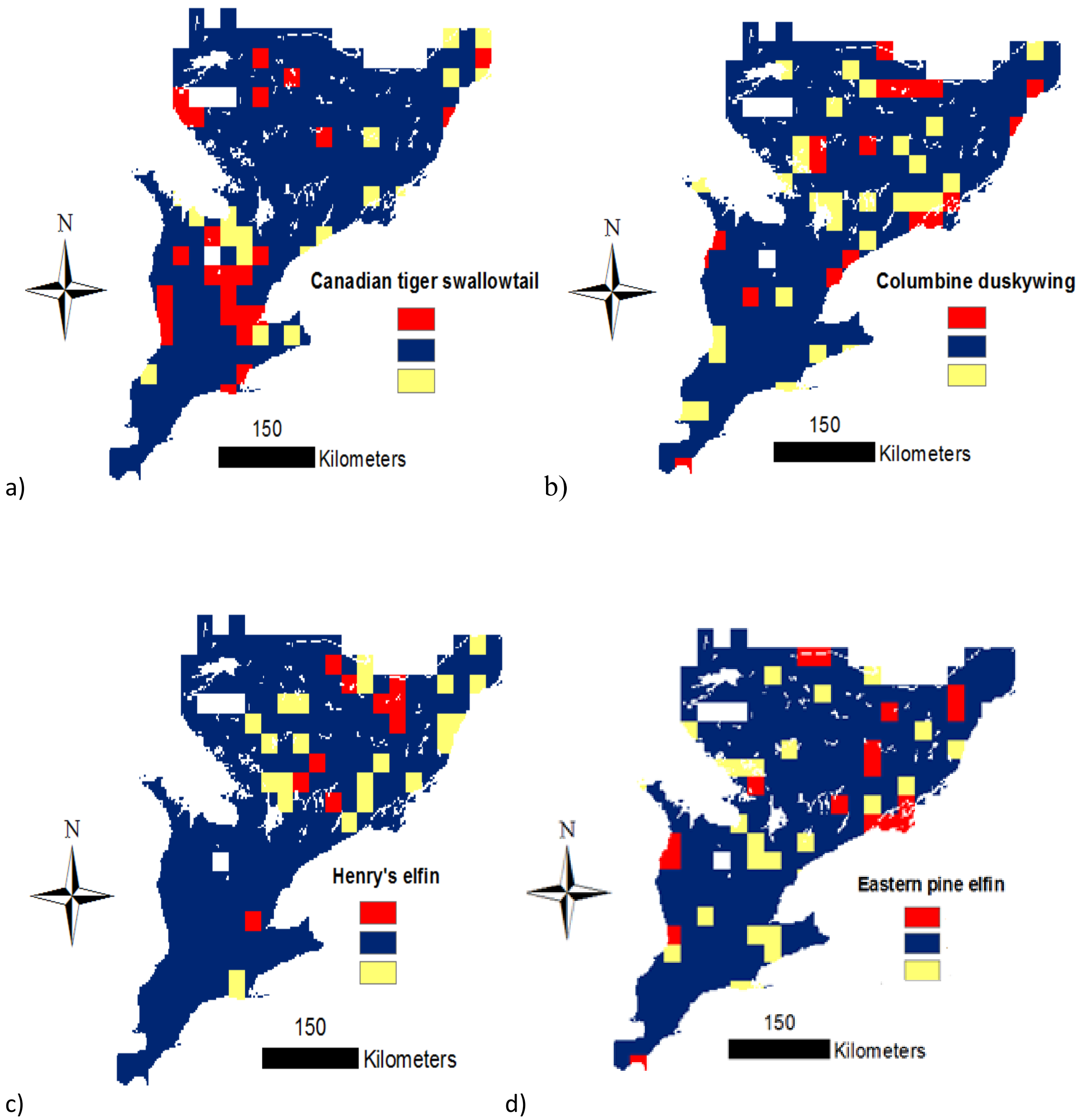

Figure 4a-d: Simulated current distribution from the logistic model (threshold proabability of occurrence $p \geq 0.5$) at 25km x 25km. Blue squares indicates simulated presence coinciding with observed presence; red squares indicate that the model predicted presence in quadrats where the species was absent and yellow indicates the model failed at predicting presence. Panel A) Canadian tiger swallowtail (*Papilio canadensis*), b) Columbine duskywing (*Erynnis lucilius),* c) Henry's elfin (*Callophrys henrici) and* d) Eastern pine elfin (*Callophrys niphon).*

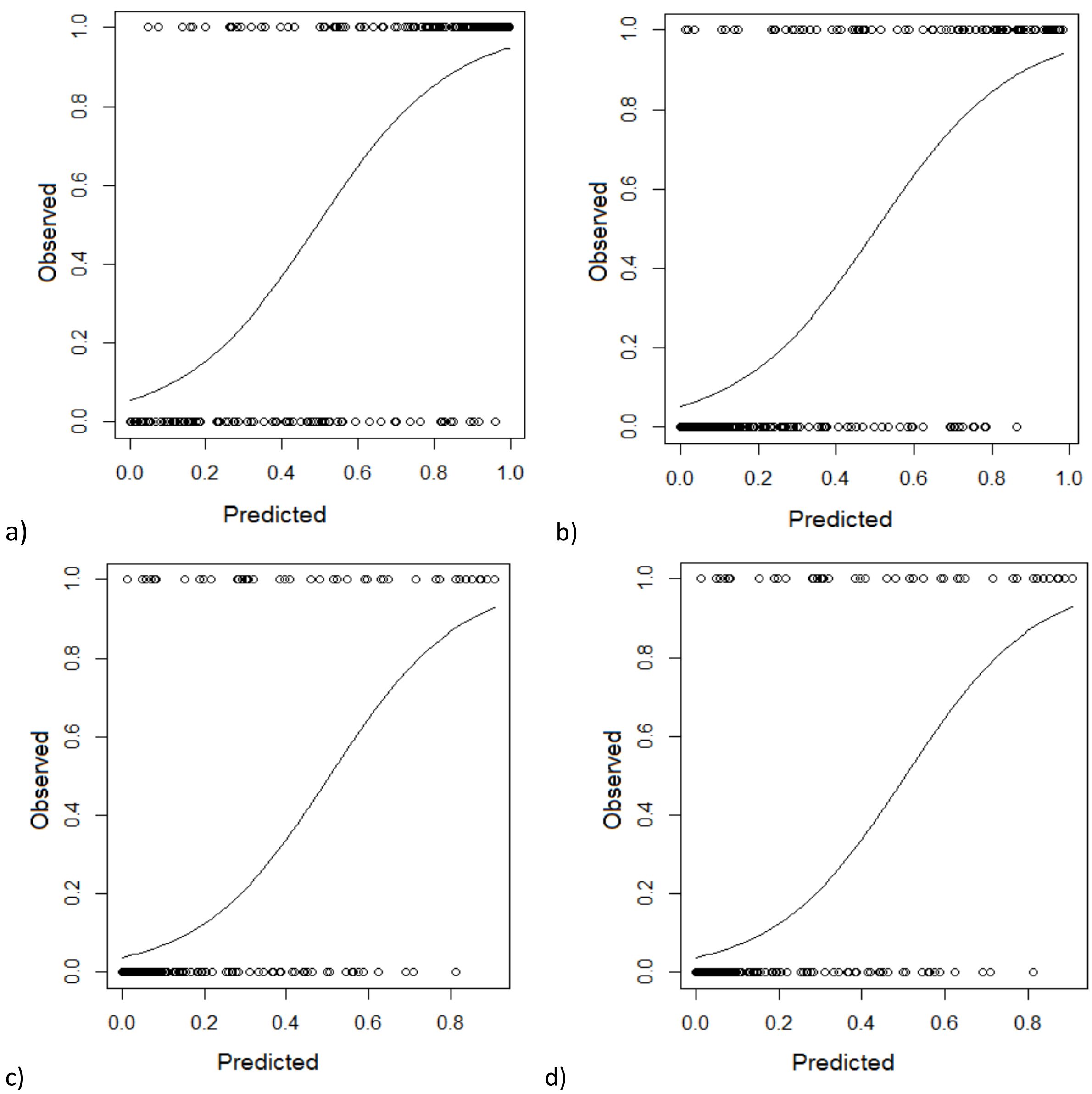

Figure 5: Observed species presence/absence as a function of the predicted values for : a)The Canadian tiger swallowtail (*Papilio canadensis*), b) Columbine duskywing (*Erynnis lucilius),* c) Henry's elfin (*Callophrys henrici) and* d) Eastern pine elfin (*Callophrys niphon).*

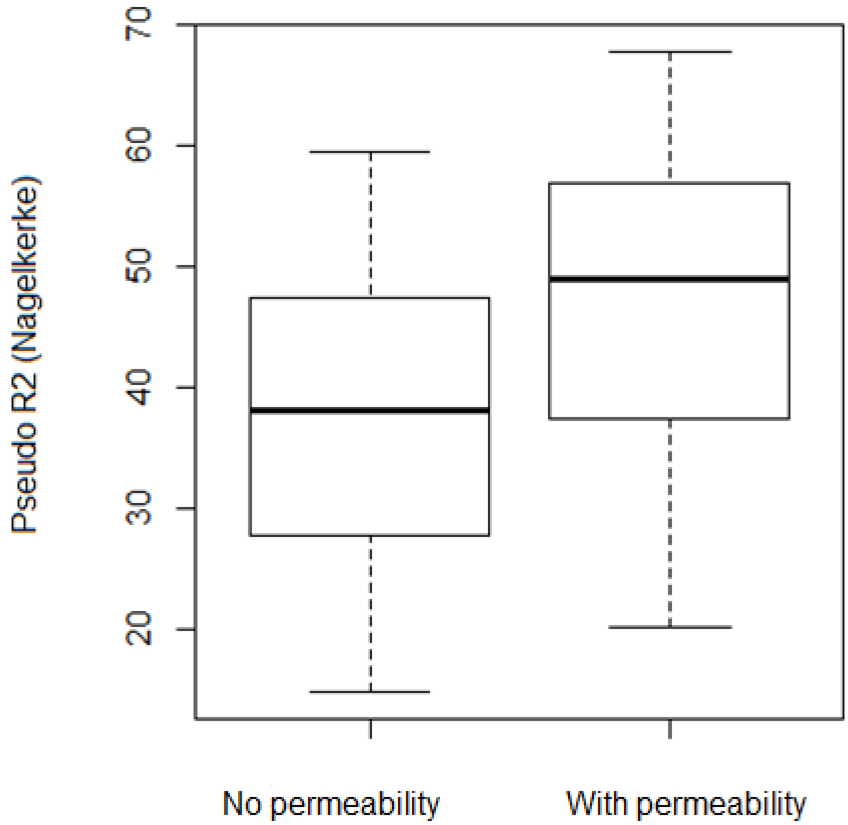

Figure 6: The pseudo-R^2 (Nagelkerke) for the models with and without permeability for the species (46) that showed a significant effect of permeability (paired t-test: mean= 8.541, p = <<< 0.05).

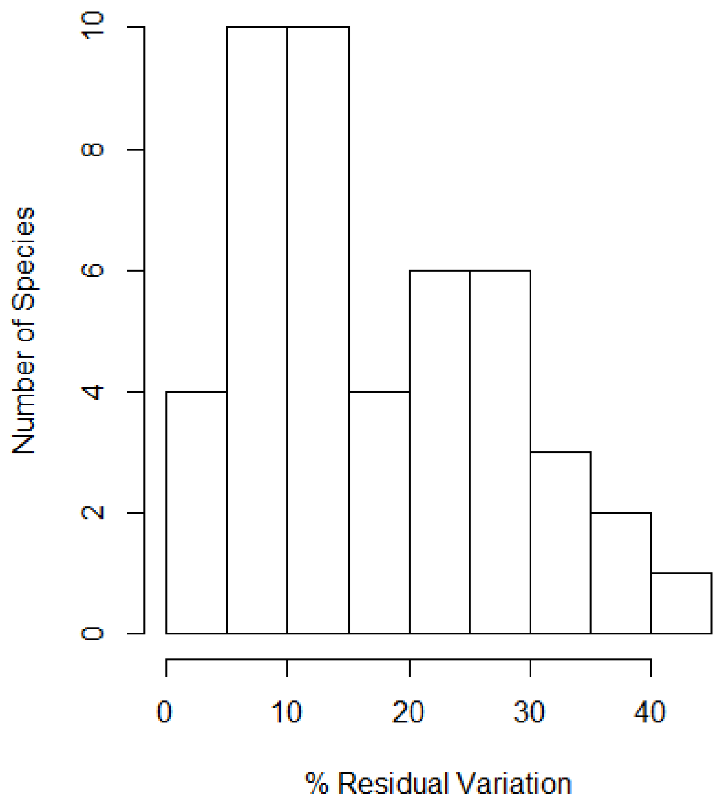

Figure 7: The proportion of residual variation explained by incorporating permeability for the 46 species with a significant main effect of permeability or interaction between temperature and permeability.

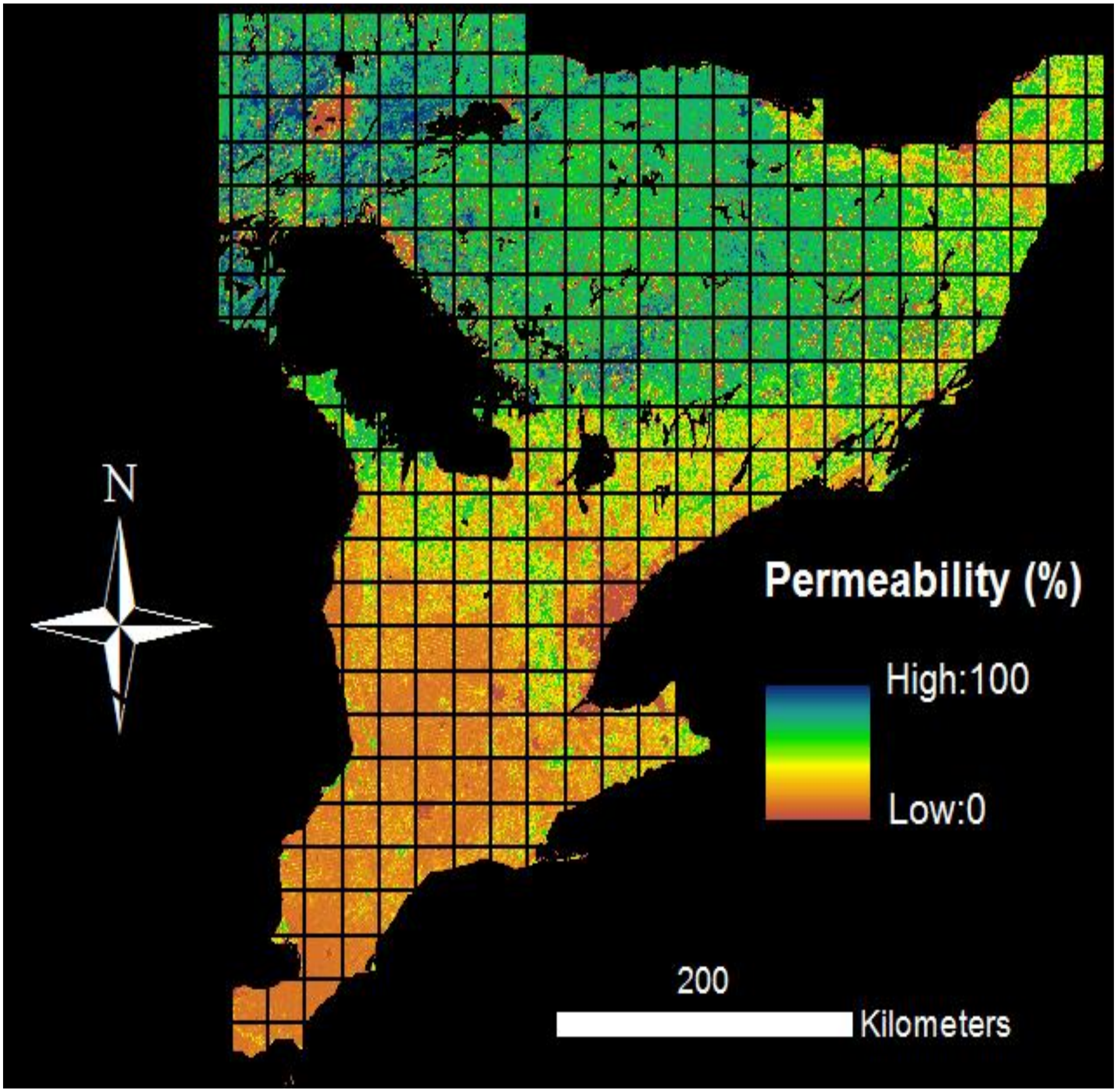

Figure 8: Broad-scale gradient of landscape permeability for 100 butterfly species. This map was produced by combining the 100 species-specific permeability measurements and averaged across pixels (100m) to map permeability for the assemblage of butterfly species. Areas where permeability is low provide target regions for landscape-level conservation efforts in order to facilitate climate change induced range shifts.

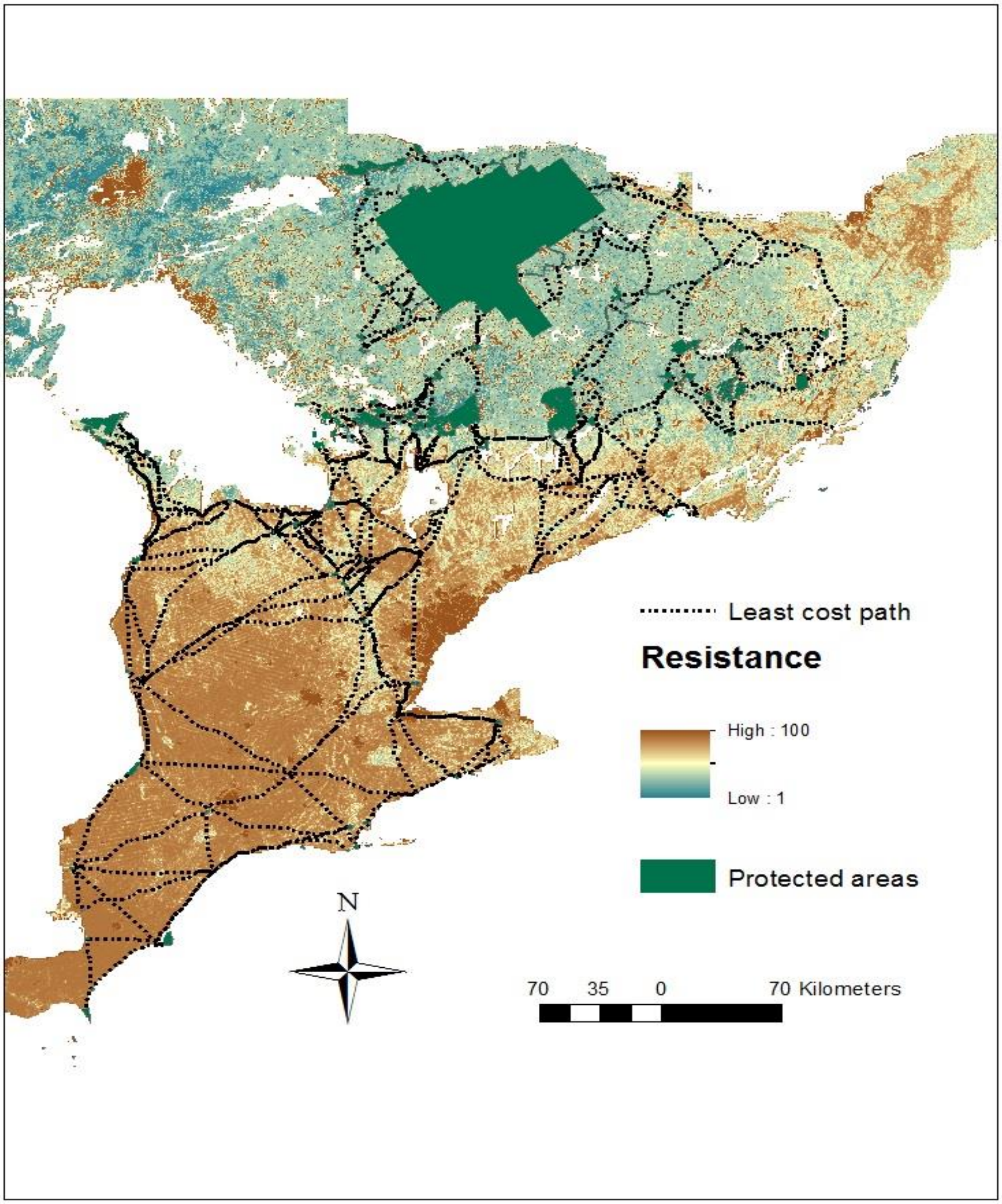

Figure 9: Connected network of protected areas produced by creating least cost paths (Euclidean and cost-weighted distance) between the protected areas throughout the study region. The connectivity analysis used the mapped resistance layer in the background which represents the relative "cost" of passing through the gridded mapped surface (100m x 100m). The resistance layer was created by averaging across pixels (100m x100m) the 100 species-specific permeability maps and taking the inverse so that higher values indicate a higher "cost".

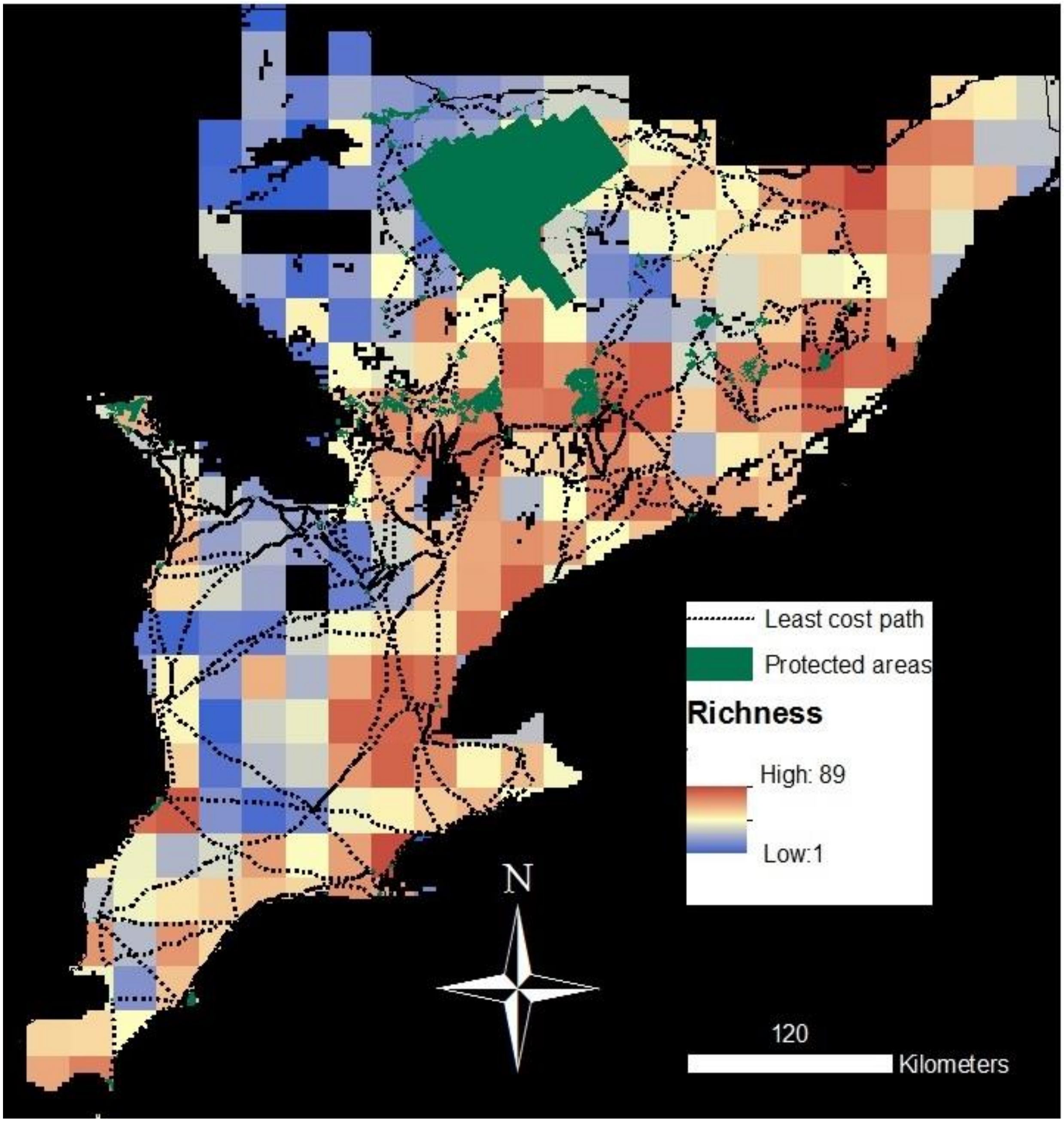

Figure 10: Identifying conservation priorities for spatial landscape planning under climate change. We combined fine- scale data to model least cost paths with observed coarse-scale butterfly species richness. Least-cost paths between protected areas that intersect areas of high butterfly species richness represent regions where increased connectivity in the form of climate corridors will be most valuable for biodiversity conservation. Some of the protected areas throughout the study region are too small to see in this map.

APPENDIX A.

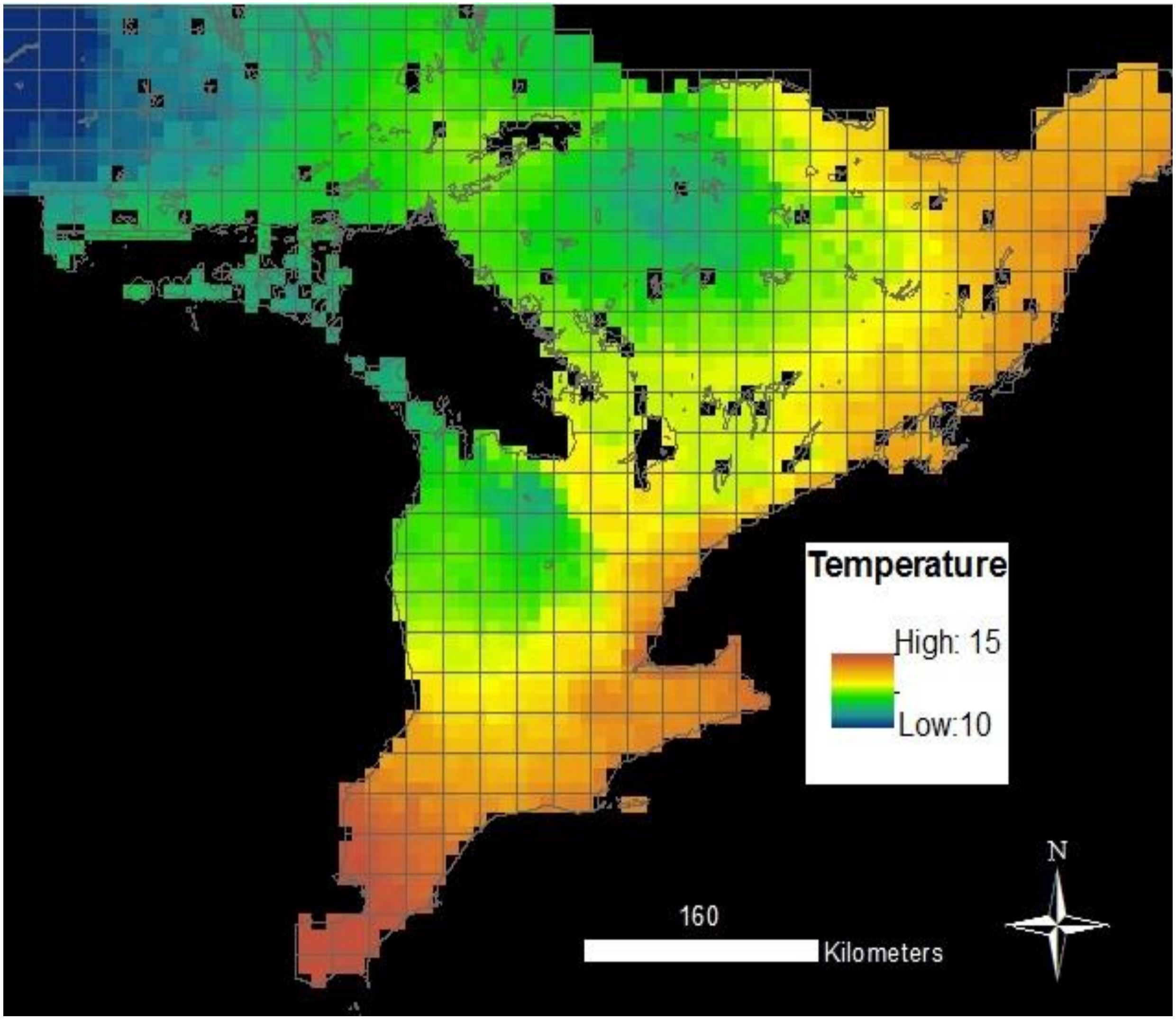

Figure A1: The monthly mean temperature for the growing season at 5 arc-minute resolution from 1960-2012 were combined to produce the spatial variation of temperature across the study region. The grid network of 25km x25km was used to extract mean temperature for each quadrat.

Appendix B: Species-specific habitat suitability

Table 1: Reclassification of the land covers from the Ontario Provincial-Scale Land Cover data set to potentially suitable habitat for each of the 96 butterfly species used in the analysis. The land covers are: inland marsh (5), deciduous swamp (6), coniferous swamp (7), open fen (8), treed fen (9), open bog (10), treed bog (11), dense deciduous forest (13), dense coniferous forest (14), coniferous plantation (15), mixed forest that is mainly deciduous (16), mixed forest that is mainly coniferous (17), sparse coniferous forest (18), sparse deciduous forest (19), recent cutovers (20), recent burns (21), old cuts and burns (22), mine tailings, quarries and bedrock outcrops (23), settlement and developed land (24), pasture and abandoned fields (25), cropland (26) and alvar (a dry grassland, 27). Land covers that may potentially include suitable habitat are coded as 1 and those that do not are coded as 0.

Family	Scientific name	Common name	5	6	7	8	9	10	11	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Pieridae	*Colias philodice*	Clouded sulphur	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
Hesperiidae	*Polites peckius*	Peck's skipper	1	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	1
Nymphalidae	*Asterocampa celtis*	Hackberry emperor	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	1	1	0	1
Hesperiidae	*Hylephila phyleus*	Fiery skipper	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1
Hesperiidae	*Pholisora catullus*	Common sootywing	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	1
Lycaenidae	*Cupido comyntas*	Eastern tailed-blue	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	1
Nymphalidae	*Polygonia interrogationis*	Question mark	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
Hesperiidae	*Thymelicus lineola*	European skipper	1	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	1
Pieridae	*Colias eurytheme*	Orange sulphur	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
Papilionidae	*Papilio cresphontes*	Giant swallowtail	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	0	0
Papilionidae	*Papilio polyxenes*	Black swallowtail	1	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	0	1
Hesperiidae	*Polites themistocles*	Twany-edged skipper	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1
Nymphalidae	*Satyrodes appalachia*	Appalachian brown	0	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
Hesperiidae	*Erynnis icelus*	Dreamy duskywing	0	1	1	0	0	0	0	1	1	0	1	1	1	1	1	1	1	0	0	0	0	0
Hesperiidae	*Pompeius verna*	Little glassywing	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	0	1
Hesperiidae	*Wallengrenia egeremet*	Northern broken-dash	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	0	1
Lycaenidae	*Lycaena hyllus*	Bronze copper	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nymphalidae	*Vanessa cardui*	Painted lady	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1
Nymphalidae	*Aglais milberti*	Milbert's tortoiseshell	1	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	0	0
Papilionidae	*Papilio troilus*	Spicebush swallowtail	0	1	1	0	0	0	0	1	1	1	0	1	1	1	1	1	1	0	0	0	0	0

Pieridae	*Pyrisitia lisa*	Little yellow	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	1
Lycaenidae	*Satyrium liparops*	Striped hairstreak	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	0	1	0	0
Nymphalidae	*Vanessa virginiensis*	American lady	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	1	0	1
Hesperiidae	*Anatrytone logan*	Delaware skipper	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1
Nymphalidae	*Boloria bellona*	Meadow fritillary	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1
Hesperiidae	*Epargyreus clarus*	Silver-spotted skipper	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
Hesperiidae	*Euphyes vestris*	Dun skipper	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	1	0	0	0
Pieridae	*Pontia protodice*	Checkered white	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1
Lycaenidae	*Satyrium acadica*	Acadian hairstreak	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Nymphalidae	*Speyeria cybele*	Great spangled fritillary	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	0	0	1	0	1
Hesperiidae	*Thorybes pylades*	Northern cloudywing	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
Hesperiidae	*Ancyloxypha numitor*	Least skipper	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hesperiidae	*Euphyes dion*	Dion skipper	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nymphalidae	*Junonia coenia*	Common buckeye	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1
Lycaenidae	*Satyrium titus*	Coral hairstreak	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	0	1
Papilionidae	*Papilio glaucus*	Eastern tiger swallowtail	0	1	0	0	0	0	0	1	0	0	1	1	0	1	1	1	1	0	0	0	0	0
Hesperiidae	*Erynnis baptisiae*	Wild indigo duskywing	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	1	1	0	1
Lycaenidae	*Satyrium calanus*	Banded hairstreak	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1	1	1	0	1	0	0	0
Lycaenidae	*Satyrium edwardsii*	Edward's hairstreak	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1
Hesperiidae	*Poanes hobomok*	Hobomok skipper	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1	1	1	0	0	0	0	0
Hesperiidae	*Polites mystic*	Long dash	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Nymphalidae	*Cercyonis pegala*	Common wood-nymph	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	0	1

Hesperiidae	*Erynnis juvenalis*	Juvenal's duskwing	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1	1	1	0	0	0	0	0
Nymphalidae	*Vanessa atalanta*	Red admiral	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1
Nymphalidae	*Limenitis archippus*	Viceroy	0	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
Nymphalidae	*Polygonia comma*	Eastern comma	1	1	1	0	0	0	0	1	1	0	1	1	1	1	1	1	1	0	0	0	0	0
Nymphalidae	*Megisto cymela*	Little wood-satyr	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	0	1
Hesperiidae	*Polites origenes*	Crossline skipper	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	0	1
Nymphalidae	*Nymphalis antiopa*	Mourning cloack	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1
Lycaenidae	*Celastrina neglecta*	Summer azure	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1	1	0	0	0	1	0	1
Nymphalidae	*Satyrodes eurydice*	Eyed brown	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nymphalidae	*Chlosyne nycteis*	Silver checkerspot	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	1	0	0
Hesperiidae	*Euphyes conspicua*	Black dash	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lycaenidae	*Lycaena phlaeas*	American copper	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	0	1
Lycaenidae	*Celastrina lucia*	Northern azure	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1	1	1	0	0	0	0	0
Nymphalidae	*Speyeria aphrodite*	Aphrodite fritillary	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	0	1
Nymphalidae	*Phyciodes cocyta*	Northern crescent	1	0	0	0	0	0	0	1	1	0	1	1	1	1	1	1	1	1	0	1	0	0
Lycaenidae	*Strymon melinus*	Gray hairstreak	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	1	1	1
Nymphalidae	*Euphydryas phaeton*	Baltimore checkerspot	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nymphalidae	*Enodia anthedon*	Northern pearly-eyes	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1	1	1	0	0	0	0	0
Lycaenidae	*Feniseca tarquinius*	Harvester	0	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
Pieridae	*Pieris rapae*	Cabbage white	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1
Hesperiidae	*Poanes massasoit*	Mulberry wing	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hesperiidae	*Poanes viator*	Broad-winged skipper	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Hesperiidae	*Erynnis lucilius*	Columbine duskywing	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
Hesperiidae	*Hesperia leonardus*	Leonard's skipper	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	0	1
Lycaenidae	*Satyrium caryaevorus*	Hickory hairstreak	0	0	0	0	0	0	0	1	0	0	1	1	0	1	1	1	1	0	0	0	0	0
Hesperiidae	*Euphyes bimacula*	Two-spottedskipper	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nymphalidae	*Boloria selene*	Silver bordered-fritillary	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hesperiidae	*Amblyscirtes hegon*	Pepper and salt skipper	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
Nymphalidae	*Coenonympha tullia*	Common ringlet	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	0	1
Nymphalidae	*Nymphalis J-album*	Common tortoiseshell	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
Lycaenidae	*Callophrys gryneus*	Juniper hairstreak	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	1
Nymphalidae	*Polygonia progne*	Gray comma	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
Lycaenidae	*Glaucopsyche lygdamus*	Silvery blue	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	0	1
Hesperiidae	*Amblyscirtes vialis*	Common roadside- skipper	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1
Lycaenidae	*Callophrys polios*	Hoary elfin	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	0	1
Nymphalidae	*Chlosyne harrisii*	Harris' checkerspot	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Nymphalidae	*Phyciodes batesii*	Tawny crescent	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	1	0	1
Pieridae	*Euchloe olympia*	Olympia marble	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	0	1
Lycaenidae	*Callophrys augustinus*	Brown elfin	0	0	0	0	0	1	1	0	1	1	1	1	1	0	1	1	1	0	0	0	0	0
Lycaenidae	*Callophrys niphon*	Eastern pine elfin	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	1	1	0	0	0	0	0
Hesperiidae	*Hesperia sassacus*	Indian skipper	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	1	0	1
Papilionidae	*Papilio canadensis*	Canadian tiger swallowtail	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1	1	1	0	0	0	0	0

Nymphalidae	*Limenitis arthemis*	White admiral	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
Pieridae	*Pieris virginiensis*	West virginia white	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0
Pieridae	*Pieris oleracea*	Mustard white	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
Nymphalidae	*Polygonia faunus*	Green comma	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
Nymphalidae	*Speyeria atlantis*	Atlantis fritillary	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
Hesperiidae	*Carterocephalus palaemon*	Arctic skipper	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	0	0
Lycaenidae	*Lycaena epixanthe*	Bog copper	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pieridae	*Colias interior*	Pink-edged sulphur	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
Lycaenidae	*Callophrys henrici*	Henry's elfin	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
Lycaenidae	*Callophrys eryphon*	Western pine elfin	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	1	1	0	0	0	0	0
Nymphalidae	*Oeneis chryxus*	Chryxus arctic	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	0	1
Nymphalidae	*Boloria eunomia*	Bog fritillary	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX C: Developing species-specific permeability measurements (used as an indicator for habitat fragmentation)

Due to the difficulty of quantifying habitat fragmentation, there are many proxies that are used to test for its effects on species (Fahrig 2003). The most commonly used proxies (i.e. edge density, number of patches) do not include the influence of the surrounding matrix, are measurements that offer a purely structural representation of the landscape (Öckinger et al. 2011, Kupfer 2012) and are often not species-specific (Krauss et al. 2003). In our study we used landscape permeability (synonymous to "functional connectivity") (Kupfer 2012, Ziółkowska et al. 2014) because it is a direct measurement that captures how landscape elements influence species dispersal. We applied a grid- based approach to represent species-specific landscape permeability across the study region. This is a more ecologically oriented approach for quantifying landscape structure because it takes into account the response of species to landscape elements (Kupfer 2012).

Permeability was mapped as a continuous surface by assigning a value to each pixel based on the theoretical spread of a species from a focal pixel is a function of the "cost" of moving across that cell (conductance surface layer) and the connectivity of that cell to the surrounding landscape (i.e. potential sources for dispersing individuals).

Step1- Construction of the generalized conductance layer:

To estimate resistance to movement, we resampled the land cover dataset to 100m, in order to speed up processing while maintaining a biologically meaningful resolution, and converted it into a conductance surface. A conductance travel surface estimates the ease with which species can cross a given land cover type (Koen et al. 2012, Graves et al. 2014). Higher values indicate low cost to dispersal and low values indicate high cost to dispersal. Parameterization of a conductance surface by applying a cost weight to different land cover types is very challenging because the cost of movement through a land cover type is species-specific and the true cost is rarely known (Koen et al. 2012, Graves et al. 2014). Although costs should be based on species-specific biological information, generalized conductance surface layers are often used when the analysis involves a large assemblage of species and data of species-specific dispersal in different land cover types are lacking (Koen et al. 2012). A general assumption is made that natural habitats are relatively less resistant to dispersal than more human-dominated habitats (Lizée et al. 2012, Fernández-Chacón et al. 2014) and more natural habitats (where human impact is minimal) promote species persistence and colonization. Based on this assumption, we created a generic conductance surface layer where land-cover types were grouped into categories based on increasing naturalness and conductance coefficients were assigned to those categories. Land-cover types were grouped into three major categories: the first group consisted of natural habitat land-cover types and received the highest value of conductance (i.e. least costly, high dispersal habitat suitability), the second group consisted of agricultural fields, and the third group consisted of water and impermeable surfaces (developed land) and therefore received the lowest value of conductance (i.e. most costly, low dispersal habitat suitability). Each pixel in the map received a conductance value based on the land cover category it fell into. We constructed a separate conductance surface layer for species in which dense forests present a thermal barrier. Dense forests was placed in a separate land cover category and was assigned its own conductance value because the cost associated with dispersing through dense forests should be different than the cost associated to dispersing in other natural land cover types.

Step2- Construction of species-specific connectivity measurements

The next step was to construct a connectivity gradient from the species-specific binary suitability maps that were obtained by reclassifying the land cover dataset based on species habitat preference (Appendix B). There are various metrics used in the literature to measure connectivity (Moilanen and Nieminen 2002, Kindlmann and Burel 2008). The method we chose was to quantify connectivity of a focal pixel as the amount of suitable habitat within a biologically relevant buffer distance. This provides a direct measurement of how connected the focal pixel is to the surrounding sources of potential suitable habitat for dispersing individuals. Although this is a simple measurement for connectivity, it is regularly used, has been shown to be correlated with more complex connectivity measurements (Moilanen and Nieminen 2002, Ockinger et al. 2010, Öckinger et al. 2011) and performs well at predicting colonization rates (Moilanen and Nieminen 2002, Bender et al. 2003, Bailey 2007, Ockinger et al. 2010, van Halder et al. 2015). For each pixel, we calculated the number of suitable habitat within a buffer zone surrounding the focal pixel (Figure C1). The buffer zone should be a biologically relevant size that should reflect the dispersal ability of a given species. However, dispersal knowledge about Canadian butterfly species is lacking because measuring species-specific dispersal requires extensive field, laboratory or experimental work. A meta-analysis examining the traits that affect dispersal ability in butterflies found that dispersal ranged from 29m to 600m (Sekar 2012). To avoid underestimating species' dispersal capacity, we chose 600m as the buffer zone. This may be an overly generous estimate of dispersal for some species. The end result is a species-specific connectivity gradient for 96 species.

Step3 Calculating the permeability index per pixel

We calculated a permeability index at 100m resolution across the study region by combining the generalized conductance layer and the species-specific connectivity layer. The end result is 96 species-specific continuous permeability maps where increasing values indicates increasing permeability.

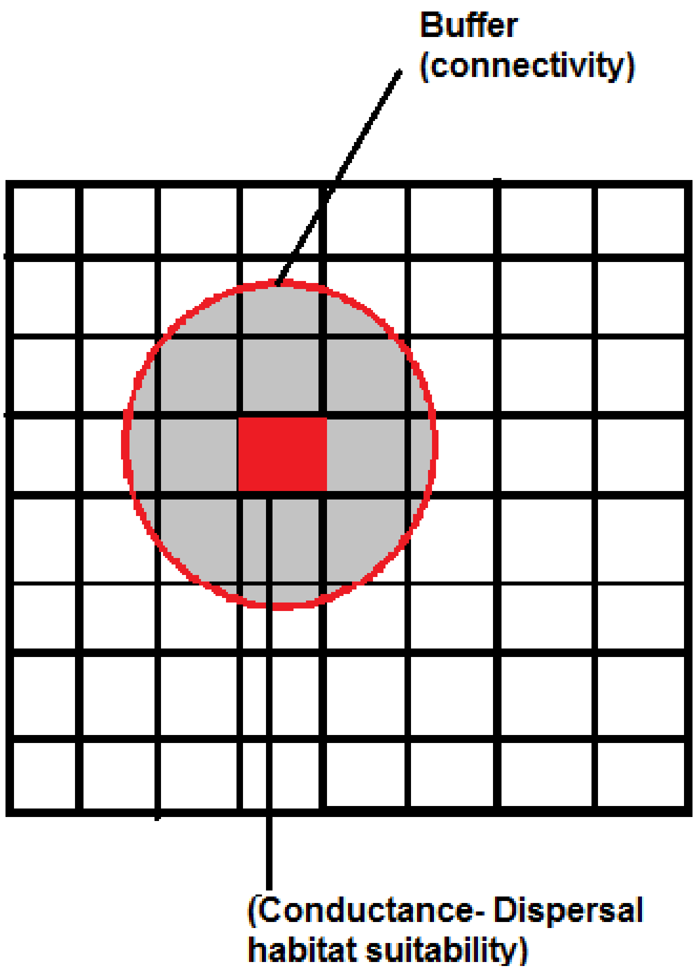

Figure C1: The moving window approach used to calculate the permeability index per pixel. Connectivity was determined by the amount of suitable habitat within the buffer zone (600m) surrounding a focal pixel. Conductance value was determined based on the land-cover category of that given focal pixel. Permeability= Connectivity X Conductance. (Esri 2011).

APPENDIX D.

Table D1: The Logistic coefficient (log-Odds) for the 46 Canadian butterfly species that showed a significant effect of permeability (direct and/or as an interaction with temperature)

Species common name	Temperature		Permeability		Temperature* permeability	
Common sootywing	0.2532	*	2.5853	**	1.8398	**
Giant swallowtail	1.3239	***	-0.5998	**	-0.1417	
Black swallotail	0.1939	*	-1.2399	***	0.3116	
Appalachian brown	0.6118	*	-0.7883	**	0.3630	
Dreamy duskywing	0.0996	*	1.0476	***	0.2790	
Bronze copper	0.6702	***	0.9896	***	-0.5876	**
American lady	-0.4357	*	0.0488		-0.7311	**
Meadow fritillary	0.3689	*	0.5243	**	0.0016	
Silver-spotted Skipper	1.4811	***	-0.0948		0.7031	*
Acadian hairstreak	0.0163		0.0458		-0.3880	*
Northern cloudywing	0.5405	*	0.9165	***	0.4446	*
Eastern tiger swallowtail	0.2426		-1.1596	***	0.1113	
Edwards hairstreak	0.5417	*	-0.1502		-0.7439	*
Juvenals duskywing	0.9997	***	1.2542	***	0.0180	
Silvery checkerspot	-1.0045	***	-0.0936		-1.0612	***
Aphrodite fritillary	-0.1861		0.8988	***	0.0629	
Northern crescent	0.4521		0.6856	*	0.3619	
Gray hairstreak	0.7879	**	-0.8961	***	0.5110	**
Northern pearly eye	0.6148	*	-0.0041		0.6291	**
Columbine duskywing	0.7309	**	1.6634	***	0.7123	**
Leonards skipper	0.1311		0.7867	***	0.4551	**
Pepper and Salt Skipper	-0.3822		1.4120	***	-0.1472	
Compton tortoiseshell	-0.2584		0.8552	***	0.3554	
Juniper hairstreak	1.3602	*	2.4435	*	-0.2517	
Gray comma	0.2349		1.0064	***	0.6850	
Silvery blue	-0.0894		1.2943	***	0.5729	**
Common roadside skipper	0.1590		2.4583	***	-0.6435	
Hoary elfin	0.0662		2.1749	**	-0.3945	
Harris checkerspot	0.7913	***	-0.2933		0.8623	***
Tawney crescent	-0.4070		0.5126	*	-0.1218	
Olympia marble	-0.5993		0.5289	**	0.0851	
Brown elfin	-0.6843	**	0.5216	*	-0.0838	
Eastern pine elfin	0.4340	*	1.5273	***	0.7312	**
Indian skipper	0.0880	*	1.1139	***	0.5330	*
Canadian tiger swallowtail	-0.3618		1.9935	***	0.7642	**
White admiral	0.7633	*	1.7681	***	1.5176	***
West Virginia white	0.8478	*	0.6191	*	0.6588	*
Mustard white	-0.5050		0.6649	**	1.2006	***

Green comma	-0.5407	*	1.2069	***	-0.2877	
Atlantis Fritillary	-0.7579	**	1.3150	***	0.1500	
Arctic skipper	-0.7410		0.7844	***	1.1598	***
Bog copper	-0.2436		0.6198	**	0.4663	
Pink-edged Sulphur	-0.6792		2.1137	***	0.5326	*
Henry's elfin	0.9683	**	1.6135	***	0.7705	**
Western pine elfin	-1.2577	*	1.4900	**	-0.0074	
Chryxus Arctic	-0.9823	*	0.7699	*	0.3343	

Significance codes: *** p < 0.001, ** p < 0.01, * p < 0.05

APPENDIX E

Table E1. Variance inflation factor (VIF) scores for the variables- observations, temperature, permeability and the interaction between temperature and permeabiltiy for the models of the 46 butterfly species that had a signficant effect of permebaility. Values of Vif exceeding 5 are considered evidence of multicollinearity.

Species ID	Observations	Temperature	Permeability	Temperature*permeability
6	1.191804	2.838954	3.202369	2.746328
12	1.10696	1.305557	1.231441	1.218163
13	1.344053	1.520828	1.775018	1.103773
15	1.162219	1.748467	1.591462	1.314961
16	1.416442	2.014472	2.012489	1.117146
19	1.000538	1.023818	2.305974	2.272788
27	1.448635	1.636072	1.662972	1.489085
29	1.093729	1.22867	1.05401	1.225053
30	1.042391	2.20099	1.436779	1.695095
34	1.10229	1.187796	1.27526	1.244372
37	1.150221	2.186127	2.279411	1.187923
42	1.262373	1.475306	1.711426	1.155496
46	1.186124	1.169714	1.398813	1.705002
50	1.258283	2.387188	2.821201	1.264982
60	1.721658	2.250843	1.334624	1.646301
64	1.486533	2.111898	1.939355	1.092409
65	1.156411	2.601652	2.505413	1.323252
66	1.133374	2.395566	2.392191	1.139946
68	1.401041	2.640025	2.233483	1.263819
74	1.360414	1.927991	2.420955	1.087833
75	1.071808	1.508457	1.549086	1.076921
80	1.590257	2.279246	1.932382	1.666073
82	1.49221	2.350569	2.315294	1.242113
83	1.002946	2.016926	3.526088	2.94909
84	1.266627	2.130779	2.285324	1.206137
85	1.574792	1.992427	2.069404	1.090654
86	1.417494	2.193317	2.439045	1.536137
87	1.302207	2.447497	1.965418	1.653308
88	1.453412	1.496862	1.519571	1.289412
89	1.21903	1.231796	1.050458	1.118552
91	1.343106	1.301901	1.171164	1.221165
92	1.483866	1.837278	1.8607	1.242382
93	1.37341	1.968118	2.516798	1.270815

94	1.344266	1.208384	1.302978	1.052344
95	1.845252	2.352612	2.736407	1.556031
96	2.601885	3.455858	4.020425	2.040113
97	1.047613	1.378537	1.309557	1.109233
98	1.43939	2.279953	2.371475	1.379264
99	2.054347	2.02333	2.200757	1.215929
100	1.879259	1.935478	2.00198	1.304141
101	1.496747	1.837674	1.699003	1.258341
102	1.235743	1.597504	1.8847	1.407896
103	1.417764	2.973951	1.42837	3.021254
104	1.287266	1.70732	2.014558	1.009897
105	1.268021	3.066545	1.733005	3.742049
106	1.564774	3.07686	1.669721	3.242756

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