Chapter 8

Impacts of land use and climate change on natural populations: The butterfly perspective

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Abstract

The past century has witnessed an explosion of anthropogenic activity, resulting in land use and climate changes on a global scale. The study of butterflies provides a unique window into the biological impacts of these changes. In this chapter, we explore several case studies that demonstrate the power of butterflies, both as model organisms in theory development and as ecological sentinels in conservation practice. These studies demonstrate how research on butterfly phenology, distribution, and diversity has yielded important insights into the interacting effects of habitat loss, fragmentation, and degradation on natural populations, as well as ecological and evolutionary responses to changing climatic conditions. Further, an important avenue for future research harnesses the power of whole-genome sequencing of butterfly populations to better document and help ameliorate biodiversity loss. Continued collaboration and knowledge transfer between dedicated amateurs and professional researchers, facilitated by humanity's innate appreciation of butterflies, will be essential to our continuing efforts to stem the catastrophic loss of biodiversity that is generally associated with modifications of natural habitats and large-scale shifts in climatic conditions.

8.1 Introduction

Anthropogenic habitat loss, habitat fragmentation, and climate change are among the greatest threats to global biodiversity (IPCC, 2021; Tilman et al., 2017; Warren et al., 2001). The scale of these threats and the rate at which they are accelerating have made it paramount that we understand and ameliorate their effects. A necessary first step is to document their impacts on specific groups of plants and animals that serve as sentinels of biodiversity change. Butterflies are among the most intensively monitored of these groups worldwide, and for good reason. Their rich history of study, variation in habitat and degree of host plant specificity, and suitability for both observational and experimental research render them ideal model organisms in conservation biology (Boggs et al., 2003). From island biogeography theory and

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metapopulation dynamics (Ehrlich and Hanski, 2004; Hanski, 1994; Hanski and Gilpin, 1991; Munroe, 1948), to mechanisms of evolution and speciation (Ehrlich and Raven, 1964; Mavárez et al., 2006; Sperling, 2003; Wallace, 1865; Watt, 2003), many theoretical advances have originated from the study of butterflies. This has often translated into real-world conservation science (Bellis et al., 2019; Boggs et al., 2003; Kremen et al., 2003). In this chapter, we explore representative case studies that demonstrate how butterflies can be used to assess anthropogenic impacts on biodiversity worldwide.

8.1.1 Why butterflies?

Everyone likes butterflies. Their charismatic nature has inspired astonishing dedication among naturalists, who have published countless books, papers, field guides, taxonomic reports, life history accounts, and detailed notes on species' distributions. This body of knowledge has facilitated deep integration and collaboration with professional scientists, promoting important knowledge transfer in both directions.

In addition to their charismatic nature, butterflies also exhibit multiple ecological and evolutionary traits that render them key sentinels of land use and climate changes. Most butterfly species have short life cycles with one or more generations per year, allowing the genetic composition and demography of populations to respond relatively quickly to changes in local habitat and environmental conditions (MacDonald et al., 2017; Nowicki et al., 2008; van Swaay & Warren, 1999). Many butterflies can live and reproduce within small fragments of habitat on landscapes modified by human activities, and their population dynamics, genetics, and diversity patterns can be used to infer the effects of habitat loss and fragmentation on ecosystem function at very fine spatial scales (MacDonald et al., 2020; van Swaay et al., 2006). A few butterfly species are migratory, such as the well-known monarch (*Danaus plexippus*) and painted lady (*Vanessa cardui*), and their study can shed light on population-level consequences of land use and climate changes at the continental scale (Flockhart et al., 2013; Miller et al., 2012; Shreeve, 1992; Stefanescu, et al., 2013). The larvae of most butterfly species are dependent on specific species of host plants as food resources, and butterfly host plant co-occurrence patterns can yield important insights into changes into multi-species ecological and trophic interactions (Filazzola et al., 2020; MacDonald et al., 2018a). Finally, the diversity of butterflies often correlates with that of other terrestrial taxa, making them viable indicators of biodiversity at the ecosystem level (MacDonald et al., 2018a; Nowicki et al., 2008; Thomas, 2005).

8.1.2 Butterfly monitoring programs

Butterfly monitoring has a long history, prominently including the 1976 establishment of the United Kingdom Butterfly Monitoring Scheme and the 1974 initiation of annual single-day butterfly counts in North America by the Xerces Society, now continued by the North American Butterfly Association (Acorn, 2017). While long-term butterfly monitoring schemes are becoming more common in a growing number of countries, the popularity of single-day butterfly counts has diminished in recent decades. For example, the number of single-day counts in Alberta, Canada, dropped from more than 40 in 2000 to around 5 in 2019 (Acorn, 2017). This decline stems, in part, from the realization that diversity data from single-day counts cannot be meaningfully compared across years. Particular species may be observed in some years but not others, and often it cannot be determined whether this is due to variation in emergence times related to weather, long-term shifts in phenology related to climate change, or actual changes to the composition of species assemblages. In contrast, other types of monitoring programs, such as 'Pollard transects' (Pollard, 1977) where counts are completed weekly or bi-weekly, provide more detailed data that can differentiate between these mechanisms (MacDonald et al., 2017; Parmesan, 2003; Westwood and Blair, 2010). The resulting data, as well as other observations from both amateurs and professionals, are now reported and organized in massive digital databases such as eButterfly (Prudic et al., 2017; www.e-butterfly.org), the Global Biodiversity Information Facility (GBIF; www.gbif.org), and iNaturalist (www.inaturalist.org). Open access with no paywall to these databases allows researchers to quantify changes in species' phenologies, distributions, and overall diversity patterns at spatial and temporal scales that are otherwise impossible (Acorn, 2017; MacDonald et al., 2017).

8.2 Effects of land use change on butterfly populations

In the Anthropocene, perhaps the most immediate threat to biodiversity is land use change (Brooks et al., 2002; Hanski, 2011). Global extinction rates are estimated to be 100–1000 times more than they were before intensive human activity, and much of this increase can be attributed to modification or destruction of natural habitats through urbanization, agriculture, and forestry (Pimm et al., 2014; Rosenzweig, 1995). In the majority of ecosystems around the world, effects of these anthropogenic activities are negative for native species, and this holds true for butterflies (Boggs et al., 2003; Tabarelli et al., 2012; Warren et al., 2001). However, some butterfly species depend on specific host plants and diverse nectaring plants that occur in non-forested habitats, meaning anthropogenic disturbances actually increase butterfly abundance and diversity in particular circumstances (reviewed by Dover and Settele, 2009). For example, Riva et al. (2018a) found that clearing boreal forests along seismic lines for oil exploration in Alberta, Canada, generally increases the overall abundance and diversity of butterflies (but see Riva et al., 2018b) for negative effects on the disturbance-sensitive species, the cranberry blue, *Plebejus optilete*). In another example, Thomas (1991) showed that butterfly species occurring throughout the UK are dependent on high-frequency disturbance regimes that facilitate open forest canopies and early successional plant assemblages. These types of habitats were far more prevalent on landscapes 4500–10,000 BP during warmer climatic conditions, but are now primarily maintained by agricultural practices (Dennis, 1993; Thomas, 1991; Vera, 2000). Continuation of some agricultural practices may therefore be necessary for the persistence of particular butterfly species (Singer and Parmesan, 2018; Singer et al., 1993). However, in the majority of cases, butterflies are negatively affected by land use changes that lead to extensive habitat loss, fragmentation, and degradation.

8.2.1 Habitat loss and fragmentation

Examples of worldwide habitat loss are astonishing. More than 94% of Earth's temperate broadleaf forests have been modified or destroyed by human development (Primack, 2006). Approximately 85% of natural habitat throughout Europe has been modified or destroyed (Primack, 2006), more than 97% of North America's tallgrass prairies have been converted to farmland (White et al., 2000), and more than 50% of wetlands in the USA and 60–70% in Europe have been drained (Ravenga et al., 2000). As of 2021, less than 16% of Earth's terrestrial landmass has been explicitly set aside for conservation and legally protected from human development (UNEP-WCMC IUCN, 2021). Given this modest percentage of protected habitat, conservation biologists are particularly concerned with how its spatial configuration (i.e. degree of fragmentation) affects biodiversity. Human activities often leave behind isolated fragments of natural habitat, from small pockets of undeveloped land to larger nature reserves. While habitat loss has unequivocally negative effects on species diversity, the interconnected fields of theoretical ecology and conservation biology are marked by a vigorous debate on whether habitat fragmentation poses additional threats. The study of butterflies has contributed much to this debate.

8.2.2 Some history

Relationships between habitat fragmentation and biodiversity have interested conservation biologists since Levins' (1969) extrapolation of the theory of island biogeography to habitat fragments on terrestrial landscapes (Haila, 2002). Although the theory is generally attributed to a collaboration between Robert MacArthur and Edward Wilson (MacArthur and Wilson, 1963; Wilson and MacArthur, 1967), its basic tenets were preceded by Eugene Munroe (1948) in his doctoral work on butterflies of the West Indies (Brown and Lomolino, 1989). Munroe (1948) observed that the number of butterfly species observed on oceanic islands may represent an equilibrium between the opposing processes of colonization and extinction, each of which is principally determined by an island's area and isolation. This was a harbinger of MacArthur and Wilson's (1963) theory of island biogeography, which predicts that larger and less isolated islands harbor more species due to lower extinction and higher immigration rates, while smaller and more isolated islands harbor fewer species due to higher extinction and lower immigration rates.

The application of the theory of island biogeography to conservation is intuitive and appealing. If edges of terrestrial habitat fragments delimit populations similar to the shores of oceanic islands, small populations occupying small fragments may be more prone to extinction than larger populations occupying unfragmented habitat (Diamond, 1975). Most butterfly species have minimum area requirements for sustaining viable populations (reviews in Crone and Schultz, 2003; Dover and Settele, 2009), suggesting that at least at the lower size limit the analogy holds. For example, Crone and Schultz (2003) calculated that Fender's blue (*Icaricia icarioides fenderii*), an endangered butterfly endemic to upland prairies in Oregon, requires a fragment area of >6 ha for long-term population persistence. The increased ratio of edge-to-area that results from smaller patch sizes may also degrade the quality of remaining habitat for species that are particularly sensitive to habitat edges (Hadley and Betts 2016; Ries and Sisk, 2004).

The theory of island biogeography also predicts that species diversity is affected by the isolation of habitat fragments. As the distance between habitat fragments increases, they will be less likely to receive immigrants belonging to new species or exchange individuals of resident species that may be important for demographic health and avoiding inbreeding depression. Butterflies have served as model organisms for quantifying these isolation effects, with numerous studies investigating effects of inter-fragment distances on metapopulation dynamics and genetic differentiation (e.g. Hanski, 1994, 1999; Keyghobadi et al., 2005; Kuussaari et al., 1996; MacDonald et al., 2020; Matter et al., 2003). For many species with limited mobility, even modest levels of isolation reduce or eliminate inter-fragment movements (e.g. 300 m for the scarce heath (*Coenonympha hero*); Cassel et al., 2001). For long-term species persistence on these landscapes, the area of habitat fragments must be greater than that required to support a minimum viable population (Crone and Schultz, 2003; MacDonald et al. 2018a).

By these and related mechanisms, habitat fragmentation may result in a greater loss of species than that resulting from habitat loss alone. This has many conservation biologists concerned (reviewed by Fletcher et al., 2018). However, it is becoming increasingly recognized that many inferences of negative fragmentation effects are based on observations and study designs that have not decoupled the correlated effects of habitat fragmentation and habitat loss (Fahrig, 2003, 2013, 2017; Hadley and Betts, 2016). Habitat fragmentation is almost always accompanied by habitat loss, which may in fact be the primary driver of diversity declines on landscapes modified by anthropogenic activities. To effectively control for these confounding effects, many researchers have framed habitat fragmentation in terms of the 'SLOSS' debate, which asks whether the configuration of protected lands as 'Single Large Or Several Small' habitat fragments protects a greater number of species (Diamond, 1975). Because many butterflies respond quickly to changes in habitat configuration and are able to live and reproduce within small habitat fragments, they serve as an excellent indictor group for evaluating SLOSS at fine temporal and spatial scales.

8.2.3 Butterfly case studies

Many studies have used butterflies to infer effects of habitat loss, fragmentation, and quality on species diversity. Here we explore two studies that quantify patterns of butterfly diversity on a naturally fragmented landscape of lake islands (MacDonald et al., 2018a, 2021). True islands provide interesting models for investigating the effects of fragment area and isolation on species diversity (Dover and Settele, 2009; Haila, 2002). From more than 14,500 islands in Lake of the Woods, Canada, MacDonald et al. (2018a) selected 30 islands, in two sets of 15, based on their area (Figure 8.1). The small island set contained one 0.8 ha island, two 0.4 ha islands, four 0.2 ha islands, and eight 0.1 ha islands. Here, the single 0.8 ha island represented 0.8 ha of unfragmented habitat, the two 4.0 ha islands represent 0.8 ha of moderately fragmented habitat, the four 2.0 ha islands represent 0.8 ha of more fragmented habitat, and the eight 1.0 ha islands represent 0.8 ha of highly fragmented habitat. The large island set followed the same basic design, but was comprised of islands 10 times larger; one 8.0 ha island, two 4.0 ha islands, four 2.0 ha islands, and eight 1.0 ha islands. This study design effectively decouples degree of habitat fragmentation from total habitat area, or, in other words, habitat fragmentation from habitat loss. Species richness and the relative abundance of butterfly species on each of the 30 islands were quantified using repeated full-island surveys, with sampling effort standardized per unit area.

Thirty-four butterfly species were observed across all islands. Surprisingly, in both island sets, the combined diversity of several small islands was approximately equal to the diversity of the single large island of equal total area (Figure 8.2). This result was also found with other SLOSS-based methods that assessed fragmentation effects across all 30 islands simultaneously, such as comparisons of species accumulation curves (MacDonald et al., 2018a). In this analysis, cumulative species richness is plotted against cumulative island area in two ways: (1) adding islands, one at a time, from the largest island to smallest island (large-to-small curve); and (2) adding islands, one at a time, from the smallest island to largest island (small-to-large curve) (Figure 8.3). For any value of cumulative island area along the x-axis of the plot, the cumulative species richness of single/few larger islands and

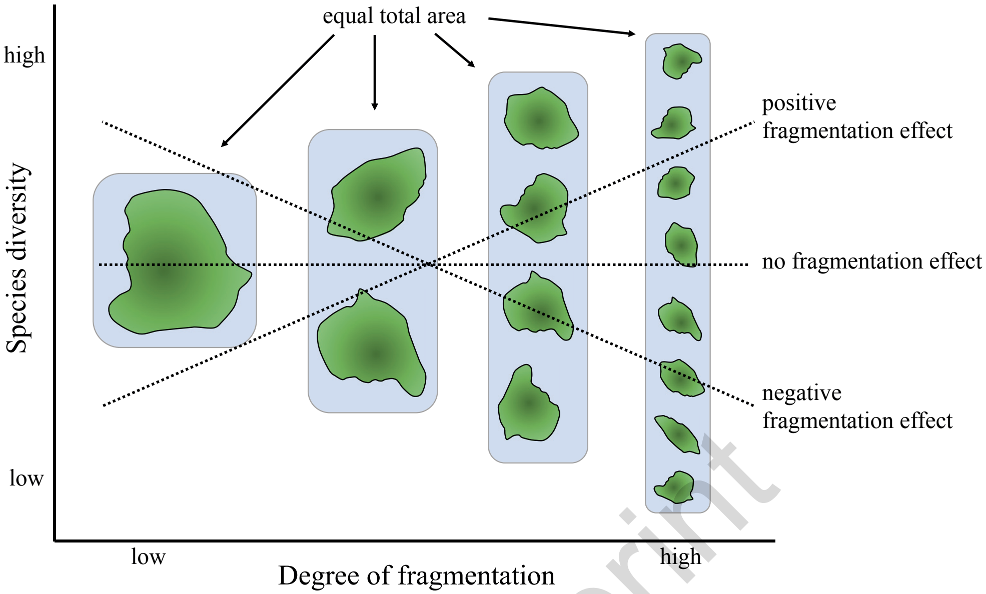


Figure 8.1 Experimental design of MacDonald et al. (2018a, 2018b), showing how sets of islands or habitat fragments, differing in their individual areas and number of replicates, can be used to decouple the effects of habitat fragmentation from habitat loss. Total habitat area is maintained between four groupings of islands, but degree of fragmentation increases from left to right. If species diversity decreases, does not change, or increases across increasing degrees of fragmentation, it can be inferred that fragmentation has a negative effect, no effect, or positive effect, respectively.

several small islands, equal in their total areas, can be compared by examining the difference between the large-to-small and small-to-large curves. Considering all butterflies observed across the 30 study islands, the large-to-small and small-to-large curves are nearly identical, indicating that single/fewer larger and several small islands contain the same number of butterfly species (Figure 8.3a). This equates to a neutral fragmentation effect. Additionally, after controlling for island area, generalized linear models resolved that isolation was not significantly related to species richness. Together, these results suggest that decreasing fragment area and increasing fragment isolation do not affect butterfly diversity after controlling for total habitat area.

These results accord with predictions of Fahrig's (2013) 'habitat amount hypothesis', which posits that the number of species persisting on fragmented landscapes is solely a function of habitat loss and not its degree of fragmentation. The primary mechanism underlying the habitat amount hypothesis is the sample-area effect, which describes that species richness increases with island/fragment area only because larger islands/fragments randomly sample more individuals from the regional species pool (Connor & McCoy, 1979). In other words, the species-area relationship is just a sampling artefact; if a researcher surveys a larger area, they will find more species simply because of their increasing sampling effort. To date, the majority of SLOSS-based studies addressing a plethora of taxa (e.g., plants, insects, birds, mammals) have found that several small islands or habitat fragments contain an equal or greater number of species compared to single large

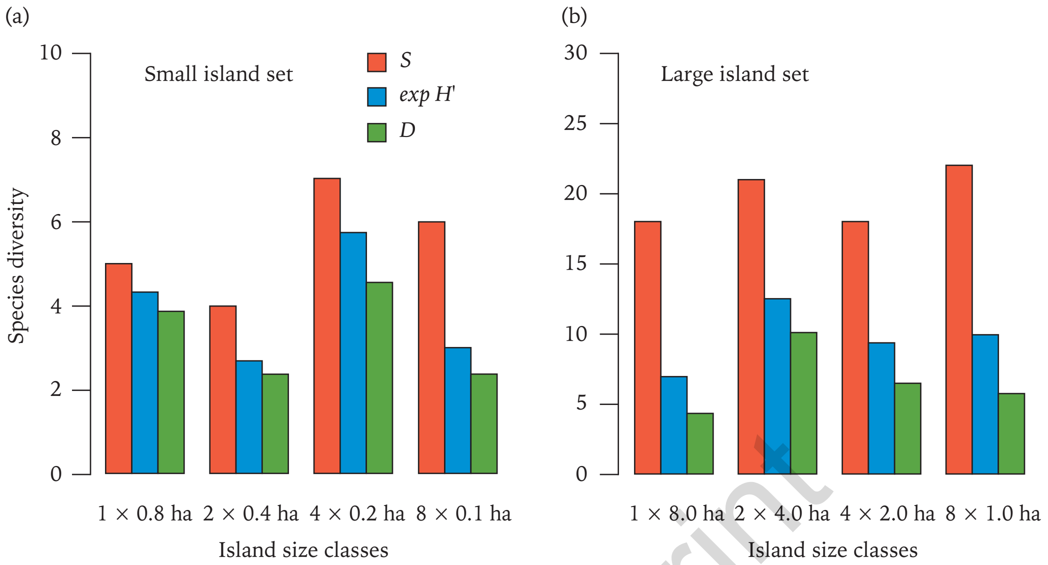


Figure 8.2 Butterfly species richness (*S*), the exponential of the Shannon-Wiener index (exp *H*′), and Simpson's reciprocal index (*D*) for island size classes that represent different degrees of habitat fragmentation while controlling for total habitat area (MacDonald et al., 2018a). Within each of the two island sets (panels a and b), island size classes varied in degree of fragmentation while maintaining an equal total area. There was no obvious change in the diversity of butterflies across island size classes, suggesting that habitat fragmentation does not affect butterfly diversity after controlling for habitat loss.

islands/fragments (reviewed in Fahrig, 2003; 2013; 2017).

Although SLOSS-based studies based on overall patterns of species diversity often report neutral or even positive effects of fragmentation, such inferences may be susceptible to ecological fallacy (*sensu* Robinson, 1950). This addresses biases that may arise when observed effects on aggregated variables (e.g. species richness) differ from causal relationships at finer levels of organization (e.g. occurrences of single species) (MacDonald et al., 2021). Populations respond to external conditions, such as degree of habitat fragmentation, and species richness sometimes emerges in misleading ways. This point is demonstrated by a disparity in the findings of a thorough review of the fragmentation literature. Fahrig (2017) found that 90% (114/127) of studies addressing patterns of species diversity (generally, species richness) inferred a positive effect of fragmentation. However, studies that addressed responses of individual species were much more varied in their results, with only 68% (158/232) reporting positive fragmentation effects (Fahrig, 2017). Greater congruence in the results of studies addressing species diversity and those addressing individual species would be expected if patterns of species diversity are indeed viable indicators of fragmentation effects on individual species. This suggests that analyses of species diversity may obscure important species-level fragmentation effects.

Looking deeper into butterfly diversity patterns on islands of Lake of the Woods, it became apparent that occurrences of butterfly species with small wingspans were generally restricted to large islands that contained their host plant species (MacDonald et al., 2018a). In other words, small species were excluded from

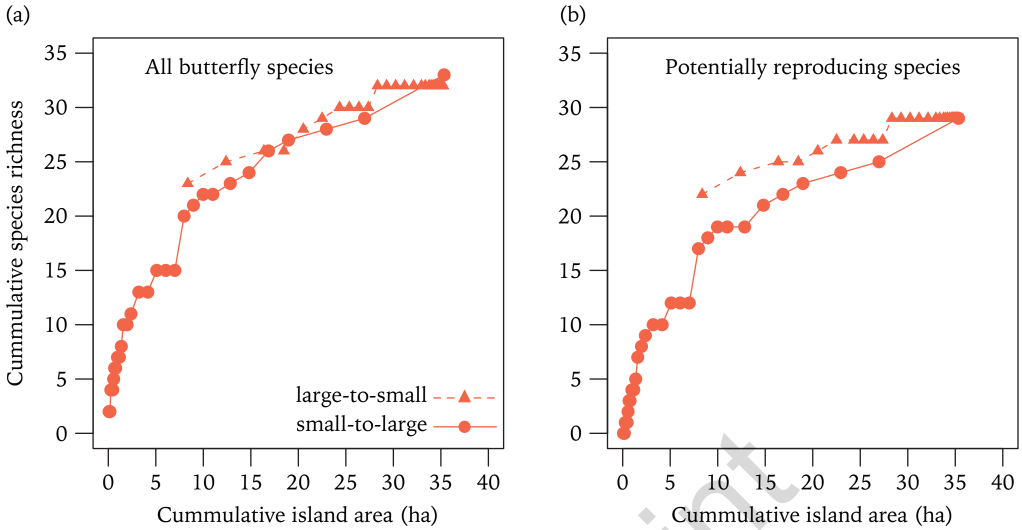
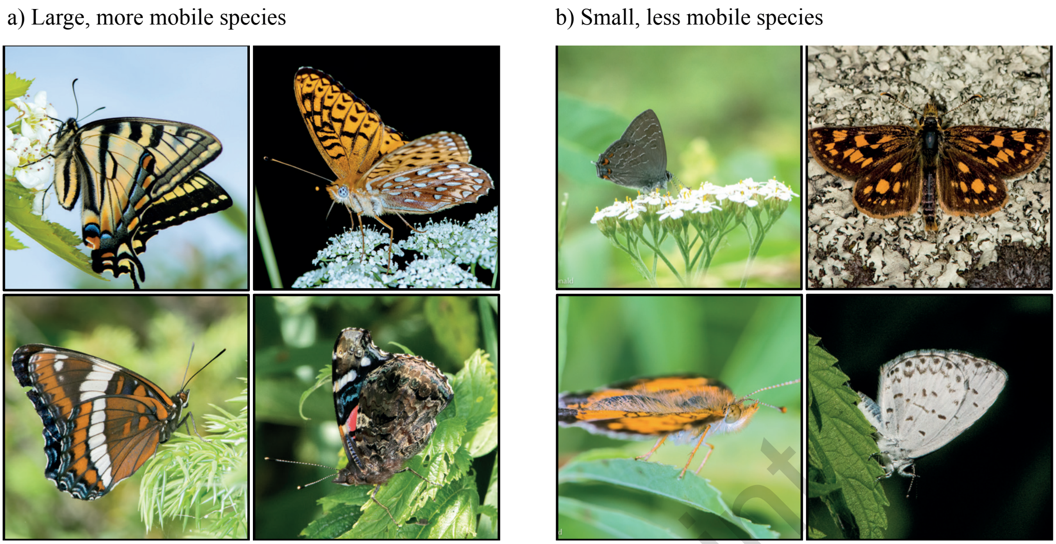


Figure 8.3 Species accumulation curves inform whether single/fewer large islands harbor a greater or lesser number of species than many small islands of equal total area (MacDonald et al., 2018a; 2018b). This was completed for both total butterfly species richness (a) and for the richness of potentially reproducing species only (described below) (b). In each panel, cumulative species richness is plotted against cumulative island area in two ways: 1) by adding islands, one at a time, from the largest to smallest island (large-to-small curve; triangles connected by dashed lines); and 2) adding islands, one at a time, from the smallest to largest island (small-to-large curve; circles connected by solid lines). For any value of cumulative island area along the x-axis, the cumulative species richness of single/fewer large islands and many small islands of equal total area can be compared by examining the difference between the two curves. When all butterfly species were included in the analysis (a), overlap of the two curves indicates that single/fewer large islands and many small islands of equal total area contain the same number of species. However, when transient individuals were removed (b), the large-to-small curve accumulated species more quickly than the small-to-large curve, indicating that single/fewer large islands support a greater number of potentially reproducing species than many small islands of equal total area.

particularly small islands and islands of any size that lacked their host plants. In contrast, butterfly species with large wingspans frequented islands of all sizes, regardless of whether their host plants were present or absent. Wingspan is one of the strongest predictors of butterfly species' mobility and dispersal ability (Burke et al., 2011). Accordingly, MacDonald et al. (2018a) hypothesized that movements of larger and highly mobile 'transient' species from large islands (containing host plants) to smaller islands (lacking host plants) may be obscuring important effects of habitat fragmentation on species diversity (examples in Figure 8.4). In a re-analysis of the data, MacDonald et al. (2018a) removed from the dataset all individuals occurring on islands that did not contain their host plant species, as these individuals cannot represent reproducing populations. Rerunning SLOSS-based analyses on 'potentially reproducing' species only, negative fragmentation effects became very apparent: comparisons of species accumulation curves showed that several small islands harbored fewer potentially reproducing


a) Large, more mobile species

b) Small, less mobile species

Figure 8.4 Examples of butterflies observed on a naturally fragmented landscape of lake islands; Lake of the Woods, Ontario, Canada. (a) Four large and more mobile butterfly species generally found on islands of all sizes, regardless of the presence of their larval host plants (from top left, clockwise: Canadian tiger swallowtail (*Papilio canadensis*); atlantis fritillary (*Speyeria atlantis*); red admiral (*Vanessa atalanta*); white admiral (*Limenitis arthemis*)). (b) Four small and less mobile species that were generally excluded from both small islands and islands of any size that lacked their host plants (from top left, clockwise: striped hairstreak (*Satyrium liparops*); arctic skipper (*Carterocephalus palaemon*); summer azure (*Celastrina neglecta*); northern crescent (*Phyciodes cocyta*)). Occurrence and abundance patterns of these butterflies across lake islands show that habitat fragmentation disproportionally affects small and less mobile species (MacDonald et al., 2018a, 2021). Photos by Zachary G. MacDonald.

species than single large islands (Figure 8.3b). Additionally, generalized linear models resolved that island isolation had a significant effect on species richness after transient individuals were removed from the dataset. MacDonald et al. (2018a) therefore suggested that inter-fragment movements, but not breeding or establishment of self-sustaining populations, of large, highly mobile butterfly species inflate the total number of species observed on small habitat fragments, obscuring important fragmentation effects.

Differentiating between the richness of transient versus potentially reproducing butterfly species hinted that an autecological (i.e. species-by-species) approach may be most effective for inferring effects of habitat fragmentation on butterflies. Butterfly species can vary considerably in their responses to landscape factors and researchers are particularly interested in morphological, behavioral, and ecological characteristics of butterflies that might explain this variation (Dover and Settele, 2009). Functional traits, including body size, mobility and dispersal ability, perceptual range, degree of ecological specialization, rarity/conservation status, and trophic position are hypothesized to relate to species' sensitivity to habitat fragmentation for a variety of taxa (see references in MacDonald et al., 2019, 2021). However, few studies have tried to relate functional traits to interspecific variation in fragmentation effects, or model how this interspecific variation scales to emergent patterns of species diversity on fragmented landscapes.

To address this knowledge gap, MacDonald et al. (2021) reanalyzed the Lake of the Woods butterfly data with a novel methodological framework, using random placement models (instead of SLOSS-based methods) to control for the sample-area effect while integrating functional trait analyses. These analyses showed that habitat fragmentation may have negligible effects on overall butterfly species richness, in agreement with the previous SLOSS-based analyses. However, applying the new methods to individual butterfly species identified a number of important fragmentation effects that were not previously detected. For many butterfly species, probabilities of occurrence were lower than predicted by the sample-area effect for small islands. This indicates that small islands are of lower habitat quality than larger islands, suggesting an important fragmentation effect. Even more prominent were effects on butterfly species' abundances, which were much lower on both smaller and more isolated islands than predicted by the sample-area. Most importantly, the analyses demonstrated that negative fragmentation effects were significantly greater for smaller and less mobile butterfly species, highlighting the importance of individual species traits in fragmentation research.

In sum, the relative size and mobility of butterfly species can be a strong predictor of their sensitivity to fragmentation (and see Dover and Settele, 2009). Individual habitat fragments may contain resources sufficient for the persistence of some butterfly species, but not others. Large and highly mobile species may be able to move among multiple habitat fragments to meet their resources requirements, rendering them more resilient to habitat fragmentation. To adequately evaluate fragmentation effects on species diversity, it is important to differentiate transient individuals from resident individuals representing established populations. Different butterfly species are affected by habitat fragmentation in different ways, and autecological details need to be considered when we evaluate the effects of habitat fragmentation on butterflies. The habitat amount hypothesis is generally unsupported for butterflies, and we suggest that efforts to minimize habitat fragmentation and abate habitat loss remain as foundations in conservation practice.

8.3 Habitat degradation

Many terrestrial landscapes fragmented by anthropogenic activities are more complex than true island systems (Haila, 2002). For example, the terrestrial matrix that separates isolated fragments is often variable and less hostile than open water, and may in fact be the preferred habitat of some matrix-dwelling species (Riva et al., 2018a). The quality of individual habitat fragments themselves can also vary widely due to habitat degradation. Along with total habitat area, habitat quality is often a principal factor determining the persistence of many butterfly species on landscapes fragmented or otherwise modified by anthropogenic activity. For example, rather than area *per se*, larval habitat quality and isolation were the strongest predictors of fragment occupancy for the Glanville fritillary (*Melitaea cinxia*), Adonis blue (*Polyommatus bellargus*), and Lulworth skipper (*Thymelicus acteon*) in the UK (Thomas et al., 2001). Furthermore, large populations inhabiting high-quality (rather than large) habitat fragments have been inferred to facilitate colonization/recolonization of adjacent, unoccupied fragments, helping to stabilize species' metapopulations (Thomas et al., 2001). Habitat quality was also the principal factor affecting the assemblage of grassland butterfly species inhabiting isolated habitat fragments in an urban-dominated landscape in the UK (Wood & Pullin, 2002), and habitat quality and area, but not isolation, were the principal factors governing the distribution of Alcon blue (*Maculinea alcon*) across 127 habitat fragments in the Netherlands (Wallis DeVries, 2004). Notwithstanding these observations of the importance of habitat quality, both Wenzel et al. (2006) and Öckinger and Smith (2006) observed that species richness and overall abundance of grassland butterflies on fragmented agricultural landscapes were strongly related to their isolation from semi-natural grassland habitats. As with the two studies addressing butterfly assemblages on islands of Lake of the Woods (MacDonald et al., 2018a, 2021), small, less mobile species were most sensitive to fragmentation effects in two these studies.

8.3.1 Interacting effects of ecology and evolution

Land use changes can also affect the evolution of butterfly species, threatening their long-term persistence. A particularly rigorous history of research on Edith's checkerspot (*Euphydryas editha*) has resulted in inferences of eco-evolutionary processes that affect species persistence. For example, Singer and Parmesan (2018) found that an isolated population of *E. editha* in Nevada, USA, shifted its primary host plant association from *Collinsia parviflora*, the historical native host, to *Plantago lanceolata*, a non-native species introduced by cattle ranchers. Such host shifts in *E. editha* were first documented in the 1980s, with female *E. editha* rapidly evolving a preference for ovipositing on *Plantago* in heavily grazed landscapes due to higher larval survival (Singer et al., 1993). Some populations even abandoned *Collinsia* completely and evolved total dependence on *Plantago*.

However, it has become clear that the survival of *Plantago*-feeding populations may be heavily dependent on continued cattle grazing. Due to the sale of private land, grazing was eventually stopped on the landscape inhabited by the isolated Nevada population, allowing tall grasses to grow around the *Plantago* plants. The resulting shading drastically reduced survival of the thermophilic *E. editha* larvae, which would have otherwise survived on *Collinsia* occupying drier microhabitats that were unaffected by grazing. Although *Collinsia* was still present on the landscape, female *E. editha* did not switch back to ovipositing on it. Shortly after grazing ceased, Singer and Parmesan (2018) documented that the entire *E. editha* population, which had completely switched its host association from *Collinsia* to *Plantago*, went extinct. This extinction was the product of an 'eco-evolutionary trap', set by anthropogenic activity. Although the area was eventually recolonized by adjacent *Collinsia*-feeding *E. editha* populations, this is a particularly instructive example of the complex effects of land use changes and the possibility for unintended consequences of reclamation practices. Butterflies adapting to land use changes risk becoming dependent on continuation of the same practices. Indeed, Singer et al. (1993, p. 681) warn that 'This is a serious risk, because human cultural evolution can be even faster than the rapid genetic adaptation that the insects can evidently achieve.'

In sum, effects of land use changes on butterflies are complex and often difficult to predict. Different butterfly species can respond to similar land use changes in very different ways; some species are lucky 'winners' and succeed in changing landscapes, while the unfortunate majority are likely to be 'losers' suffering population declines and possibly extinction (Filgueiras et al., 2021; Tabarelli et al., 2012). Continued study of habitat loss, fragmentation and degradation will be key to understanding and possibly ameliorating these effects. However, the effects of land use changes should not be considered in isolation. Changing climatic conditions, and the rate at which these changes are accelerating, must also be taken into consideration.

8.4 Climate change

Earth's climate is changing, and anthropogenic activities are a large contributor (IPCC, 2021). Generalizable patterns include warming temperatures, increased cloud cover, and increased overall precipitation concentrated in fewer precipitation events (Easterling et al., 2000; Parmesan, 2003; Wang et al., 2016). Faced with these changes, individual populations and entire species will exhibit one of three possible responses (Parmesan, 2003).

1. Track changing climatic conditions by shifting distributions either poleward in latitude or higher in elevation.
2. Persist in the current location via phenotypic/behavioural plasticity or local adaptation to new climatic conditions.
3. Suffer extirpation or extinction.

It is generally unknown what the frequency of these three responses will be, or whether they will vary systematically across space, through time, or among taxa. Notwithstanding, the high suitability of butterflies as sentinel species for detecting, modelling, and predicting effects of climate change has been amply demonstrated in case studies on their phenology, distributions, and diversity.

8.4.1 Butterfly phenology and climate change

Butterflies are highly sensitive to abiotic conditions (Dennis, 1993; Sparks and Yates, 1997). In most mid- to high-latitude regions around the world, where butterfly species complete one or a few generations every summer, the timing of larval development, pupation, and eclosion as adults is advancing due to warming temperatures. A number of mechanisms account for this relationship. For example, faster melting of snowpacks allows butterflies (and their host plants) to begin growth and development earlier, regardless of the life stage in which they overwintered. Additionally, most temperate butterfly species are thermophilic, and the rate at which larvae grow is a function of available resources and heat, with warmer temperatures generally corresponding with faster growth rates (Singer and Parmesan, 2018). 'Growing degree days' is a commonly used measure of thermal accumulation for the development of many insects and plants. For most butterfly species, growing degree days is a better predictor of adult emergence time and overall abundance than date of the year (e.g. Cayton et al., 2015).

Around the world, emergence times of many butterfly species are shifting from historical patterns because growing day degrees are accumulating earlier in the spring as climatic conditions warm. For example, 23 butterfly species inhabiting the Central Valley of California, USA, have advanced their spring emergence times by an average of 24 days since the early 1970s (Forister and Shapiro, 2003). Changing climatic conditions in California, including temperature and precipitation, were significantly related to these phenological shifts. Similarly, data from the United Kingdom Butterfly Monitoring Scheme have shown significant advances in the emergences of multiple UK butterfly species (Sparks and Yates, 1997). Extrapolating the observed trends, regional warming of ~3°C within the next century is expected to advance the emergence of most UK butterfly species by 2 to 3 weeks. Along with earlier emergence times, flight periods of many butterfly species are becoming longer. For example, Westwood and Blair (2010) examined trends in the flight periods of 19 Canadian butterfly species and found that 13 were flying significantly longer into the autumn. With longer flight periods, we may expect some univoltine species to switch to a bivoltine life cycle, with two generations flying every summer (MacDonald et al., 2020).

8.4.2 Butterfly distributions and abundances and climate change

Butterflies were the first taxonomic group for which shifts in species' distributions and abundances were linked to changing climatic conditions. Well before anthropogenic activity was recognized to be affecting our planet's climate, butterfly enthusiasts were documenting poleward range shifts of multiple species, particularly in the UK (e.g. *Limenitus camilla*; Ford, 1945), and it was hypothesized that these range shifts were due to a general warming trend (reviewed by Dennis, 1993; Parmesan, 2003). Mean average temperatures across the UK rose by an average of 0.8°C in the 20th century, and this warming trend is predicted to continue (Murphy et al., 2009). With these types of climatic changes receiving increasing attention, research on how butterfly distributions are responding has proliferated.

A common method for inferring range shifts is to compile species' historical occurrence records and compare them to contemporary distributions. Using this approach, Burton (2003) inferred that 260 European species had experienced some degree of change in the northern limit of their occurrences since 1850. Of these, 190 exhibited a northern range expansion, while only 70 exhibited a northern range contraction. In a more thorough analysis addressing the entire ranges of 35 European butterfly species, northward shifts of both northern and southern range limits were observed for 22 species, with distances varying from 35 to 240 km (Parmesan et al., 1999). In contrast, only two species exhibited southward range shifts. In the northeastern USA, abundances of many butterfly species are increasing throughout the northern extant of their range and decreasing in the southern extent, suggesting that range shifts are underway (Breed et al., 2013).

In the absence of habitat destruction preventing movement, butterflies may continue shifting their ranges poleward as climatic conditions continue to warm (Parmesan, 2003). However, based on the limited data available, it seems that changing climatic conditions, coupled with habitat loss, fragmentation, and degradation, may exceed the resiliency of many butterfly species. In many instances, extensive habitat loss and fragmentation mean that butterfly species may be unable to track changing climatic conditions. This is predicted to result in population declines and possibly extinction. Empirical data support this prediction. For example, Warren et al. (2001) examined changes in the populations of 46 UK butterfly species that, based on previous observations, were expected to respond positively to warming temperatures. However, 34 of the 46 species experienced significant population declines over the previous 30 years. This was attributed to habitat loss and barriers to movement, which outweighed any positive effects of warming temperatures. In the Netherlands, 51 of the 72 butterfly species native to the region have experienced population declines over the 20th century, while 15 have suffered regional extinction (van Swaay and Warren, 1998). Research on Canadian butterfly distributions has also shown that while some species may be able to track changing climatic conditions via poleward shifts in their distributions, these shifts are unlikely to match the pace of changing climatic conditions for the majority of species due to their limited dispersal ability and habitat loss (Lewthwaite et al., 2018). Among these climate threatened species, those with the smallest range sizes seem to be accumulating the greatest 'climate debt', wherein northward range expansions cannot sufficiently offset southward range contractions (Lewthwaite et al., 2018). Changing climatic conditions are also having significant effects on butterfly abundances. For example, analyses of a massive dataset, including 70 survey locations across western North America, suggested that butterfly abundances have exhibited a 1.6% annual reduction over the past four decades

(Forister et al., 2021). This overall trend of fewer butterflies, as well as inter-annual fluctuations in butterfly abundance, was significantly associated with warming temperatures.

8.4.3 An autecological approach

Studying the effects of changing climatic conditions on patterns of species diversity has generated interesting hypotheses that warrant further study. However, effectively evaluating the probability of climate-induced range shifts, local adaptation, and extinction likely requires an autecological approach that considers the unique ecology and life history of individual species. *Euphydryas E. editha*, the victim of the eco-evolutionary trap studied by Singer and Parmesan (2018), has probably received more research attention in this realm than any other butterfly. One study (Parmesan, 1996) has become a landmark for quantitatively demonstrating the effects of climate change on sensitive species and their ecological associations. Examining patterns of *E. editha* population extinctions throughout western North America, from Baja California, Mexico, to British Columbia, Canada, Parmesan (1996) inferred that the species' range had shifted poleward and higher elevation by 92 km and 124 m, respectively, since the beginning of the 20th century. Most interestingly, these figures closely mirrored latitudinal and elevational shifts in temperature isotherms over the same time period, inferred to be 105 km and 105 m, respectively (Parmesan, 2003). In many correlative relationships like this, it is unclear whether butterflies are responding directly to changes in environmental conditions, or whether these relationships are mediated by intermediate variables, such as the occurrences and phenologies of host and nectar plants. However, extensive research on *E. editha* suggests that, at least for this species, the latter scenario is most likely.

For many *E. editha* populations, environmentally driven host plant senescence and its effect on larval mortality is the principal driver of abundance fluctuations (Singer, 1972; reviewed in Parmesan, 2003). In general, warm and dry climatic conditions accelerate the senescence of host plants, leaving larvae to starve if they have not reached their fourth or fifth instar and entered diapause. The effects of this can be disastrous. For example, the 1975–1977 drought in California lead to the extinction of 5 out of 21 *E. editha* populations that were being monitored at the time (Singer and Ehrlich, 1979; Ehrlich et al., 1980). Extreme weather events, which are predicted to increase in frequency with climate change, also have significant effects on abundance fluctuations and population extinctions. For example, the extinction of an entire *E. editha* metapopulation in the Sierra Nevada, California, coincided with three extreme weather events: (1) a very low winter snowpack in 1989, which caused adults to emerge earlier than nectar resources were available, leading to substantial adult mortality; (2) another very low winter snowpack in 1990, causing many early emerging adults to perish in a spring snowstorm; and (3) unseasonably cold temperatures of –5°C on 16 June 1992, which killed an estimated 97% of the metapopulation's host plant, *Collinsia*, leaving larvae to starve (Thomas et al., 1996). Following the extinction of this *Collinsia*-feeding metapopulation, the area was eventually recolonized by adjacent *Pedicularis*-feeding populations, which typically fly 2 to 3 weeks later and were less affected by these extreme weather events (reviewed by Parmesan, 2003).

While warmer and drier climatic conditions threaten the persistence of many *E. editha* populations, cooler and wetter conditions can have opposing, positive effects. In southern California, USA, and Baja California, Mexico, two consecutive years (1976 and 1977) of particularly high precipitation in the dry season led to population explosions of an endangered subspecies of *E. editha*, *E. editha quino* (Murphy and White, 1984). These high abundances were attributed to increased host plant availability and delayed host plant senescence over the two-year period. However, since then, the majority of these *E. editha quino* metapopulations have suffered extinction due to a general trend of warmer and drier conditions. Parmesan (2003) noted that, in her 1996 surveys of *E. editha quino* populations, the phenologies of larvae and local host plants were asynchronous, with host senescence preceding the hatching of larvae. As climatic conditions of this region continue to become warmer and drier, the persistence of remaining *E. editha quino* populations is questionable. Other notable threats to the subspecies include habitat loss related to urban and agricultural development, competitive exclusion of larval host plants (*Plantago*, *Antirrhinum*, and *Collinsia* spp.), and increased fire frequency. The US Fish and Wildlife Quino Checkerspot Working Group and the California Conservation Genomics Project (https://www.ccgproject.org/) are working together to identify specific conservation measures, such as population augmentation and translocation, that might aid in the persistence of *E. editha quino*. However, given the rate at which land use and climate changes are advancing in southern California and Baja California, the efficacy of these measures is uncertain.

8.4.4 Climate-induced habitat loss

An insidious effect of climate change on butterflies is climate-induced habitat loss. This is expected to be a major threat to many range-restricted, high-elevation species (Dirnböck et al., 2011), which together comprise some of the most unique species assemblages on our planet. For example, in California's Sierra Nevada, the greatest diversity of butterflies is found in non-forested habitats, such as subalpine/alpine meadows and fellfields. These unique 'sky island' habitats support three butterflies endemic to the region: the Sierra Nevada Parnassian (*Parnassius behrii*), the Sierra sulfur (*Colias behrii*), and the Ivallda Arctic (*Oeneis chryxus ivallda*). The insular nature of these species' distributions makes them particularly interesting subjects for biogeographic and genetic studies (e.g. Schoville and Roderick, 2009; Schoville et al., 2012). However, their specific habitat and environmental requirements also render them particularly sensitive to climate and habitat changes (Condamine and Sperling, 2018; Sperling et al., 2020). Many populations already occur at or near mountain tops, limiting their potential for elevational range shifts to track changing climatic conditions (Figure 8.5). Within the next century, dispersal and resultant gene flow among isolated populations will be increasingly threatened by habitat loss and fragmentation resulting from forests encroaching into subalpine/alpine habitats (Keyghobadi et al., 2005; Roland and Matter, 2007; Sperling et al., 2020). These changes are likely to threaten the persistence of high-elevation specialist species to a greater extent than sympatric generalist species (Condamine & Sperling, 2018; Dirnböck et al., 2011; Ehrlich and Murphy, 1987; Warren et al., 2001). Changing climatic conditions are also likely to impact the distribution and phenology of butterflies' host plant species, compounding their risk of extinction (Filazzola et al., 2020). In light of these predictions, effective conservation planning for alpine butterflies requires research programs that integrate methods of multiple disciplines to better understand the ecological and evolutionary processes that determine species' persistence and extinction probabilities.

8.5 A path forward: conservation and landscape genomics

A plethora of methods in landscape ecology correlate variation in the occurrences, densities,

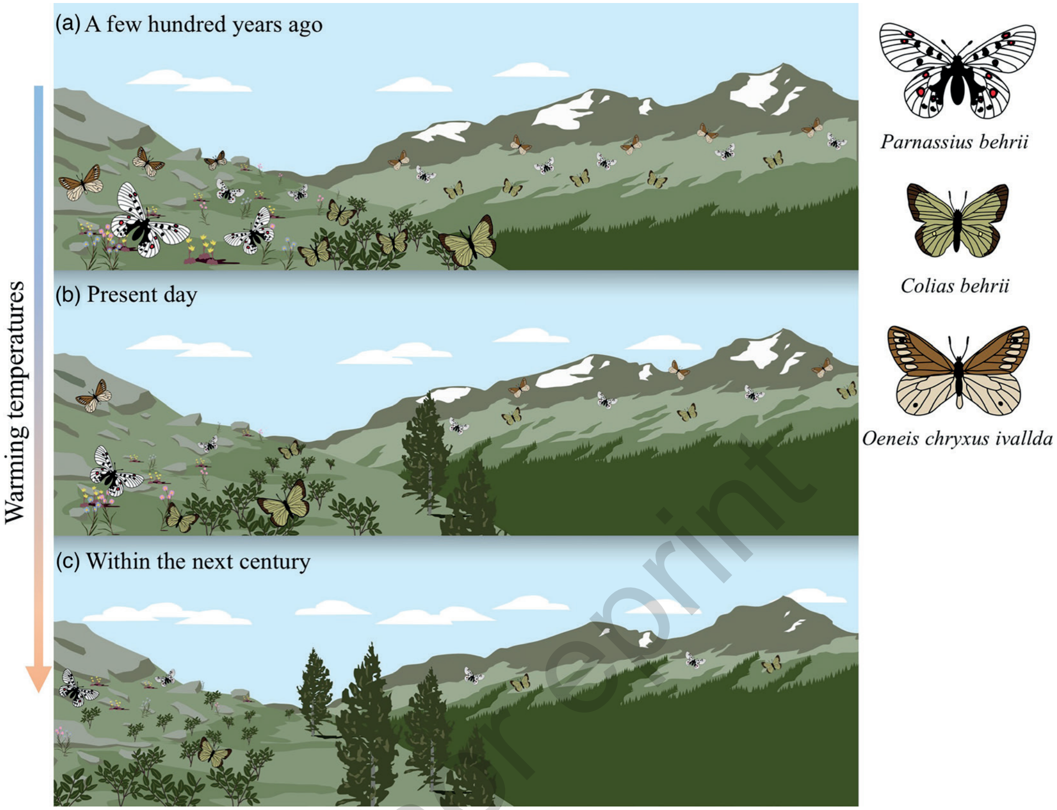


Figure 8.5 Three butterfly species endemic to the Sierra Nevada, USA: Sierra Nevada parnassian (*Parnassius behrii*), Sierra sulfur (*Colias behrii*), and Ivallda Arctic (*Oeneis chryxus ivallda*). Each of these species have highly restricted ranges and are only found in high-elevation environments such as alpine meadows and fellfields. Three panels (a, b, and c) illustrate how climate change and warming temperatures are affecting high-elevation habitats and the butterflies that depend on them. A few hundred years ago (top panel), alpine meadows and fellfields were abundant and populations of each species were well connected. Today (middle panel), warming temperatures are causing treelines to advance up mountain slopes, resulting in climate-induced habitat loss and fragmentation as alpine meadows and fellfields become smaller and further isolated. Within the next century (bottom panel), continued habitat loss, fragmentation, and degradation is expected to lead to drastic population declines and possibly extinction.

and movements of species with environmental and geographic variables to infer factors that affect species persistence. Meanwhile, advances in DNA sequencing technologies have enabled analyses of genome-wide data for almost any species of interest, helping to resolve how gene flow and adaptive genetic variation affect long-term persistence. The integration of these disciplines holds great potential, not only for understanding the effects of habitat loss, habitat fragmentation, and climate change on biodiversity, but also to aid in their amelioration through conservation planning. The emerging field of conservation genomics presents a viable toolkit for informing the conservation of imperiled butterflies and other species. An example of its application is the California Conservation Genomics Project, a state-funded initiative with a single goal: to produce the most comprehensive, multi-species, genomic dataset ever assembled to help manage regional biodiversity. This represents an intersection between genomic, landscape, and environmental methods, which together can be used to quantify the adaptive potential of threatened species and predict how their population structure and genetic health are likely to be affected by land use and climate changes.

Three endemic Sierra Nevada butterflies, along with the pipevine swallowtail (*Battus philenor*), Mormon metalmark (*Apodemia mormo*), and Edith's checkerspot (*Euphydryas editha*), are six of 236 species that are now being surveyed by the California Conservation Genomics Project. Each of these species is receiving a chromosome-level genome assembly, as well as whole-genome DNA sequencing for approximately 150 individuals. These data will be combined with forward-in-time landscape and environmental modelling to evaluate how each species is being/will be affected by land use and climate changes. The larval host plant of *B. philenor*, Dutchman's pipe (*Aristolochia californica*), is also included in this project, allowing scientists to infer how trophic interactions influence genomic patterns. Genome-wide sequence data can also be used to identify adaptive genomic variation corresponding to local environmental conditions and host associations (MacDonald et al., 2020). This information can be particularly informative for conservation practice. For example, if land use or climate changes result in the decline or extinction of populations that are of conservation concern, information on adaptive genomic variation can ensure that future translocation and reintroduction efforts focus on donor populations that are most compatible, both in terms of their ecology and genomic composition (Bellis et al., 2019). These data can also be used to inform captive breeding programs by maximizing the genetic fitness of introduced individuals.

8.6 Summary

Butterflies are unparalleled sentinels for measuring effects of land use and climate changes on biodiversity worldwide. They exhibit rapid ecological and evolutionary responses to habitat loss, fragmentation, and degradation, as well as changing climatic conditions. Detailed accounts of their phenologies, distributions, and diversity, often led by armies of engaged members of the public, have led to a pool of information available to conservation biologists that is perhaps only exceeded by birds. This knowledge has been used to infer ecological and evolutionary effects of land use and climate changes at a range of spatial scales, from habitat fragments to entire continents, and a range of temporal scales, from inter-annual population fluctuations to extinction dynamics over multiple centuries. Our society's passion for butterflies has created a unique connection between amateur naturalists and professional scientists, accelerating theoretical developments in ecology and evolution and their application to conservation practice. These continuing collaborations will be crucial to understanding and ameliorating the effects of land use and climate changes in the future, especially as we reach potential tipping points and large-scale shifts in climate patterns globally.

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References

Acorn, J. H. (2017). Entomological citizen science in Canada. *Canadian Entomologist*, *149*(6), 774–785. https://doi.org/10.4039/tce.2017.48

Baz, A., & Garcia-Boyero, A. (1995). The effects of forest fragmentation on butterfly communities in central Spain. *Journal of Biogeography*, *22*(1), 129–140. https://doi.org/10.2307/2846077

Bellis, J., Bourke, D., Williams, C., & Dalrymple, S. (2019). Identifying factors associated with the success and failure of terrestrial insect translocations. *Biological Conservation*, *236*, 29–36. https://doi.org/10.1016/j.biocon.2019.05.008

Boggs, C. L., Watt, W. B., & Ehrlich, P. R. (2003). *Butterflies: Ecology and evolution taking flight*. University of Chicago Press.

Breed, G. A., Stichter, S., & Crone, E. E. (2013). Climate-driven changes in northeastern US butterfly communities. *Nature Climate Change*, *3*(2), 142–145. https://doi.org/10.1038/nclimate1663

Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. B., Rylands, A. B., Konstant, W. R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G., & Hilton-Taylor, C. (2002). Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology*, *16*(4), 909–923. https://doi.org/10.1046/j.1523-1739.2002.00530.x

Brown, J. H., & Lomolino, M. V. (1989). Independent discovery of the equilibrium theory of island biogeography. *Ecology*, *70*(6), 1954–1957. https://doi.org/10.2307/1938125

Burke, R. J., Fitzsimmons, J. M., & Kerr, J. T. (2011). A mobility index for Canadian butterfly species based on naturalists' knowledge. *Biodiversity and Conservation*, *20*(10), 2273–2295. https://doi.org/10.1007/s10531-011-0088-y

Burton, J. F. (2003). The apparent influence of climatic change on recent changes of range by European insects (Lepidoptera, Orthoptera). *Société Royale Belge d'Entomologie*, *38*, 125–144.

Cassel, A., Windig, J., Nylin, S., & Wiklund, C. (2001). Effects of population size and food stress on fitness-related characters in the scarce heath, a rare butterfly in Western Europe. *Conservation Biology*, *15*(6), 1667–1673. https://doi.org/10.1046/j.1523-1739.2001.99557.x

Cayton, H. L., Haddad, N. M., Gross, K., Diamond, S. E., & Ries, L. (2015). Do growing degree days predict phenology across butterfly species? *Ecology*, *96*(6), 1473–1479. https://doi.org/10.1890/15-0131.1

Condamine, F. L. (2018). Limited by the roof of the world: Mountain radiations of Apollo swallowtails controlled by diversity-dependence processes. *Biology Letters*, *14*(3), 20170622. https://doi.org/10.1098/rsbl.2017.0622

Condamine, F., & Sperling, F. A. H. (2018). Anthropogenic threats to high-altitude Parnassian diversity. *News of the Lepidopterists' Society*, *60*, 94–99.

Connor, E. F., & McCoy, E. D. (1979). The statistics and biology of the species-area relationship. *American Naturalist*, *113*(6), 791–833. https://doi.org/10.1086/283438

Crone, E. E., & Schultz, C. B. (2003). Movement behaviour and minimum patch size for butterfly population persistence. In C. L. Boggs, W. B. Watt & P. R. Ehrlich (Eds.), *Butterflies: Ecology and evolution taking flight* (pp. 517–540). University of Chicago Press.

Dennis, R. L. H. (1993). *Butterflies and climate change*. Manchester University Press.

Dennis, R. L. H. (2004). Butterfly habitats, broad-scale biotope affiliations, and structural exploitation of vegetation at finer scales: The matrix revisited. *Ecological Entomology*, *29*(6), 744–752. https://doi.org/10.1111/j.0307-6946.2004.00646.x

Dennis, R. L. H., & Hardy, P. B. (2007). Support for mending the matrix: Resource seeking by butterflies in apparent non-resource zones. *Journal of Insect Conservation*, *11*(2), 157–168. https://doi.org/10.1007/s10841-006-9032-y

Diamond, J. M. (1975). The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation*, *7*(2), 129–146. https://doi.org/10.1016/0006-3207(75)90052-X

Dirnböck, T., Essl, F., & Rabitsch, W. (2011). Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Global Change Biology*, *17*(2), 990–996. https://doi.org/10.1111/j.1365-2486.2010.02266.x

Dover, J., & Settele, J. (2009). The influences of landscape structure on butterfly distribution and movement: A review. *Journal of Insect Conservation*, *13*(1), 3–27. https://doi.org/10.1007/s10841-008-9135-8

Driscoll, D. A., Banks, S. C., Barton, P. S., Lindenmayer, D. B., & Smith, A. L. (2013). Conceptual domain of the matrix in fragmented landscapes. *Trends in Ecology and Evolution*, *28*(10), 605–613. https://doi.org/10.1016/j.tree.2013.06.010

Easterling, D. R., Evans, J. L., Groisman, P. Y., Karl, T. R., Kunkel, K. E., & Ambenje, P. (2000). Observed variability and trends in extreme climate events: A brief review. *Bulletin of the American Meteorological Society*, *81*(3), 417–425. https://doi.org/10.1175/1520-0477(2000)081<0417:OVATIE>2.3.CO;2

Ehrlich, P. R., & Raven, P. H. (1964). Butterflies and plants: A study in coevolution. *Evolution*, 18(4), 586–608. https://doi.org/10.1111/j.1558-5646.1964.tb01674.x

Ehrlich, P. R., Murphy, D. D., Singer, M. C., Sherwood, C. B., White, R. R., & Brown, I. L. (1980). Extinction, reduction, stability and increase: The responses of checkerspot butterfly (*Euphydryas*) populations to the California drought. *Oecologia*, *46*(1), 101–105. https://doi.org/10.1007/BF00346973

Ehrlich, P. R., & Murphy, D. D. (1987). Conservation lessons from long-term studies of checkerspot butterflies. *Conservation Biology*, *1*(2), 122–131. https://doi.org/10.1111/j.1523-1739.1987.tb00021.x

Ehrlich, P. R., & Hanski, I. (2004). *On the wings of checkerspots: A model system for population biology*. Oxford University Press.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *34*(1), 487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Fahrig, L. (2013). Rethinking patch size and isolation effects: The habitat amount hypothesis. *Journal of Biogeography*, *40*(9), 1649–1663. https://doi.org/10.1111/jbi.12130

Fahrig, L. (2017). Ecological responses to habitat fragmentation per se. *Annual Review of Ecology, Evolution, and Systematics*, *48*(1), 1–23. https://doi.org/10.1146/annurev-ecolsys-110316-022612

Filazzola, A., Matter, S. F., & Roland, J. (2020). Inclusion of trophic interactions increases the vulnerability of an alpine butterfly species to climate change. *Global Change Biology*, *26*(5), 2867–2877. https://doi.org/10.1111/gcb.15068

Filgueiras, B. K. C., Peres, C. A., Melo, F. P. L., Leal, I. R., & Tabarelli, M. (2021). Winner–loser species replacements in human-modified landscapes. *Trends in Ecology and Evolution*, *36*(6), 545–555. https://doi.org/10.1016/j.tree.2021.02.006

Fletcher, R. J., Didham, R. K., Banks-Leite, C., Barlow, J., Ewers, R. M., Rosindell, J., Holt, R. D., Gonzalez, A., Pardini, R., Damschen, E. I., Melo, F. P. L., Ries, L., Prevedello, J. A., Tscharntke, T., Laurance, W. F., Lovejoy, T., & Haddad, N. M. (2018). Is habitat fragmentation good for biodiversity? *Biological Conservation*, *226*, 9–15. https://doi.org/10.1016/j.biocon.2018.07.022

Flockhart, D. T., Wassenaar, L. I., Martin, T. G., Hobson, K. A., Wunder, M. B., & Norris, D. R. (2013). Tracking multi-generational colonization of the breeding grounds by monarch butterflies in eastern North America. *Proceedings. Biological Sciences*, *280*(1768), 20131087. https://doi.org/10.1098/rspb.2013.1087

Ford, E. B. (1945). *Butterflies* [Reprint], 1962. Collins.

Forister, M. L., & Shapiro, A. M. (2003). Climatic trends and advancing spring flight of butterflies in lowland California. *Global Change Biology*, *9*(7), 1130–1135. https://doi.org/10.1046/j.1365-2486.2003.00643.x

Forister, M. L., Halsch, C. A., Nice, C. C., Fordyce, J. A., Dilts, T. E., Oliver, J. C., Prudic, K. L., Shapiro, A. M., Wilson, J. K., & Glassberg, J. (2021). Fewer butterflies seen by community scientists across the warming and drying landscapes of the American West. *Science*, *371*(6533), 1042–1045. https://doi.org/10.1126/science.abe5585

Hadley, A. S., & Betts, M. G. (2016). Refocusing habitat fragmentation research using lessons from the last decade. *Current Landscape Ecology Reports*, *1*(2), 55–66. https://doi.org/10.1007/s40823-016-0007-8

Haila, Y. (2002). A conceptual genealogy of fragmentation research: From island biogeography to landscape ecology. *Ecological Applications*, *12*(2), 321–334. https://doi.org/10.1890/1051-0761(2002)012[0321:ACGOFR]2.0.CO;2

Hanski, I. (1994). A practical model of metapopulation dynamics. *Journal of Animal Ecology*, *63*(1), 151–162. https://doi.org/10.2307/5591

Hanski, I. (1999). *Metapopulation ecology*. Oxford University Press.

Hanski, I. (2011). Habitat loss, the dynamics of biodiversity, and a perspective on conservation. *Ambio*, *40*(3), 248–255. https://doi.org/10.1007/s13280-011-0147-3

Hanski, I. (2015). Habitat fragmentation and species richness. *Journal of Biogeography*, *42*(5), 989–993. https://doi.org/10.1111/jbi.12478

Hanski, I., & Gilpin, M. (1991). Metapopulation dynamics: Brief history and conceptual domain. *Biological Journal of the Linnean Society*, *42*(1–2), 3–16. https://doi.org/10.1111/j.1095-8312.1991.tb00548.x

IPCC. (2021). *Climate Change 2021: The physical science basis*. https://www.ipcc.ch/report/ar6/wg1/

Keyghobadi, N., Roland, J., & Strobeck, C. (2005). Genetic differentiation and gene flow among populations of the alpine butterfly, *Parnassius smintheus*, vary with landscape connectivity. *Molecular Ecology*, *14*(7), 1897–1909. https://doi.org/10.1111/j.1365-294X.2005.02563.x

Kerr, J. T. (2001). Butterfly species richness patterns in Canada: Energy, heterogeneity, and the potential consequences of climate change. *Conservation Ecology*, *5*(1). https://doi.org/10.5751/ES-00246-050110

Krauss, J., Steffan-Dewenter, I., & Tscharntke, T. (2003). How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? *Journal of Biogeography*, *30*(6), 889–900. https://doi.org/10.1046/j.1365-2699.2003.00878.x

Kremen, C., Lees, D. C., & Fay, P. (2003). Butterflies and conservation planning in Madagascar: From patterns to practice. In C. L. Boggs, W. B. Watt & P. R. Ehrlich (Eds.), *Butterflies: Ecology and evolution taking flight* (pp. 517–540). University of Chicago Press.

Kuussaari, M., Nieminen, M., & Hanski, I. (1996). An experimental study of migration in the Glanville fritillary butterfly *Melitaea cinxia*. *Journal of Animal Ecology*, *65*(6), 791–801. https://doi.org/10.2307/5677

Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, *15*(3), 237–240. https://doi.org/10.1093/besa/15.3.237

Lewthwaite, J. M. M., Angert, A. L., Kembel, S. W., Goring, S. J., Davies, T. J., Mooers, A. Ø., Sperling, F. A. H., Vamosi, S. M., Vamosi, J. C., & Kerr, J. T. (2018). Canadian butterfly climate debt is significant and correlated with range size. *Ecography*, *41*(12), 2005–2015. https://doi.org/10.1111/ecog.03534

MacArthur, R. H., & Wilson, E. O. (1963). An equilibrium theory of insular zoogeography. *Evolution*, *17*(4), 373–387. https://doi.org/10.1111/j.1558-5646.1963.tb03295.x

MacDonald, Z. G., Nielsen, S. E., & Acorn, J. H. (2017). Negative relationships between species richness and evenness render common diversity indices inadequate for assessing long-term trends in butterfly diversity. *Biodiversity and Conservation*, *26*(3), 617–629. https://doi.org/10.1007/s10531-016-1261-0

MacDonald, Z. G., Anderson, I. D., Acorn, J. H., & Nielsen, S. E. (2018a). Decoupling habitat fragmentation from habitat loss: Butterfly species mobility obscures fragmentation effects in a naturally fragmented landscape of lake islands. *Oecologia*, *186*(1), 11–27. https://doi.org/10.1007/s00442-017-4005-2

MacDonald, Z. G., Anderson, I. D., Acorn, J. H., & Nielsen, S. E. (2018b). The theory of island biogeography, the sample-area effect, and the habitat diversity hypothesis: Complementarity in a naturally fragmented landscape of lake islands. *Journal of Biogeography*, *45*(12), 2730–2743. https://doi.org/10.1111/jbi.13460

MacDonald, Z. G., Acorn, J. H., Zhang, J., & Nielsen, S. E. (2019). Perceptual Range, Targeting Ability, and Visual Habitat Detection by Greater Fritillary Butterflies *Speyeria cybele* (Lepidoptera: Nymphalidae) and *Speyeria atlantis*. *Journal of Insect Science*, *19*(4), 1–10. https://doi.org/10.1093/jisesa/iez060

MacDonald, Z. G., Dupuis, J. R., Davis, C. S., Acorn, J. H., Nielsen, S. E., & Sperling, F. A. H. (2020). Gene flow and climate-associated genetic variation in a vagile habitat specialist. *Molecular Ecology*, *29*(20), 3889–3906. https://doi.org/10.1111/mec.15604

MacDonald, Z. G., Deane, D. C., He, F., Lamb, C. T., Sperling, F. A. H., Acorn, J. H., & Nielsen, S. E. (2021). Distinguishing effects of area *per se* and isolation from the sample-area effect for true islands and habitat fragments. *Ecography*, *44*(7), 1051–1066. https://doi.org/10.1111/ecog.05563

Matter, S. F., Roland, J., Keyghobadi, N., & Sabourin, K. (2003). The effects of isolation, habitat area and resources on the abundance, density and movement of the butterfly *Parnassius smintheus*. *American Midland Naturalist*, *150*(1), 26–36. https://doi.org/10.1674/0003-0031(2003)150[0026:TEOIHA]2.0.CO;2

Mavárez, J., Salazar, C. A., Bermingham, E., Salcedo, C., Jiggins, C. D., & Linares, M. (2006). Speciation by hybridization in *Heliconius* butterflies. *Nature*, *441*(7095), 868–871. https://doi.org/10.1038/nature04738

Miller, N. G., Wassenaar, L. I., Hobson, K. A., & Norris, D. R. (2012). Migratory connectivity of the monarch butterfly (*Danaus plexippus*): Patterns of spring re-colonization in eastern North America. *PLOS ONE*, *7*(3), e31891. https://doi.org/10.1371/journal.pone.0031891

Munroe, E. G. (1948). *The geographical distribution of butterflies in the West Indies* [PhD Thesis]. Cornell University.

Murphy, D. D., & White, R. R. (1984). Rainfall, resources, and dispersal of southern populations of *Euphydryas editha* (Lepidoptera: Nymphalidae). *Pan-Pacific Entomologist*, *60*(4), 350–354.

Murphy, J. M., Sexton, D. M. H., Jenkins, G. J., Booth, B. B., Brown, C. C., Clark, R. T., . . . & Wood, R. A. (2009). *UK climate projections science report: Climate change projections*. Met Office Hadley Centre. http://ukclimateprojections.metoffice.gov.uk/22530

Nowicki, P., Settele, J., Henry, P. Y., & Woyciechowski, M. (2008). Butterfly monitoring methods: The ideal and the real world. *Israel Journal of Ecology and Evolution*, *54*(1), 69–88. https://doi.org/10.1560/IJEE.54.1.69

Öckinger, E., & Smith, H. G. (2006). Landscape composition and habitat area affects butterfly species richness in semi-natural grasslands. *Oecologia*, *149*(3), 526–534. https://doi.org/10.1007/s00442-006-0464-6

Oliver, T. H., Marshall, H. H., Morecroft, M. D., Brereton, T., Prudhomme, C., & Huntingford, C. (2015). Interacting effects of climate change and habitat fragmentation on drought-sensitive butterflies. *Nature Climate Change*, *5*(10), 941–945. https://doi.org/10.1038/nclimate2746

Parmesan, C. (1996). Climate and species' range. *Nature*, *382*(6594), 765–766. https://doi.org/10.1038/382765a0

Parmesan, C. (2003). Butterflies as bioindicators for climate change effects. In C. L. Boggs, W. B. Watt & P. R. Ehrlich (Eds.), *Butterflies: Ecology and evolution taking flight* (pp. 541–560). University of Chicago Press.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J. K., Thomas, C. D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W. J., Thomas, J. A., & Warren, M. (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, *399*(6736), 579–583. https://doi.org/10.1038/21181

Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., Raven, P. H., Roberts, C. M., & Sexton, J. O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, *344*(6187), 1246752. https://doi.org/10.1126/science.1246752

Pollard, E. (1977). A method for assessing changes in the abundance of butterflies. *Biological Conservation*, *12*(2), 115–134. https://doi.org/10.1016/0006-3207(77)90065-9

Primack, R. B. (2006). *Essentials of conservation biology*. Sinauer.

Prudic, K. L., McFarland, K. P., Oliver, J. C., Hutchinson, R. A., Long, E. C., Kerr, J. T., & Larrivée, M. (2017). eButterfly: Leveraging massive online citizen science for butterfly conservation. *Insects*, *8*(2), 53. https://doi.org/10.3390/insects8020053

Ravenga, C., Brunner, J., Henninger, N., Kassem, K., & Payne, R. (2000). *Pilot analysis of global ecosystems: Wetland ecosystems*. World Resources Institute.

Ries, L., & Sisk, T. D. (2004). A predictive model of edge effects. *Ecology*, *85*(11), 2917–2926. https://doi.org/10.1890/03-8021

Riva, F., Acorn, J. H., & Nielsen, S. E. (2018a). Localized disturbances from oil sands developments increase butterfly diversity and abundance in Alberta's boreal forests. *Biological Conservation*, *217*, 173–180. https://doi.org/10.1016/j.biocon.2017.10.022

Riva, F., Acorn, J. H., & Nielsen, S. E. (2018b). Distribution of cranberry blue butterflies (*Agriades optilete*) and their responses to forest disturbance from in situ oil sands and wildfires. *Diversity*, *10*(4), 112. https://doi.org/10.3390/d10040112

Robinson, W. S. (1950). Ecological correlations and the behavior of individuals. *American Sociological Review*, *15*(3), 351–357.

Roland, J., & Matter, S. F. (2007). Encroaching forests decouple alpine butterfly population dynamics. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(34), 13702–13704. https://doi.org/10.1073/pnas.0705511104

Rosenzweig, M. L. (1995). *Species diversity in space and time*. Cambridge University Press.

Schmeller, D. S., Henry, P. Y., Julliard, R., Gruber, B., Clobert, J., Dziock, F., Lengyel, S., Nowicki, P., Déri, E., Budrys, E., Kull, T., Tali, K., Bauch, B., Settele, J., Van Swaay, C., Kobler, A., Babij, V., Papastergiadou, E., & Henle, K. (2009). Advantages of volunteer-based biodiversity monitoring in Europe. *Conservation Biology*, *23*(2), 307–316. https://doi.org/10.1111/j.1523-1739.2008.01125.x

Schoville, S. D., & Roderick, G. K. (2009). Alpine biogeography of Parnassian butterflies during Quaternary climate cycles in North America. *Molecular Ecology*, *18*(16), 3471–3485. https://doi.org/10.1111/j.1365-294X.2009.04287.x

Schoville, S. D., Lam, A. W., & Roderick, G. K. (2012). A range-wide genetic bottleneck overwhelms contemporary landscape factors and local abundance in shaping genetic patterns of an alpine butterfly (Lepidoptera: Pieridae: *Colias behrii*). *Molecular Ecology*, *21*(17), 4242–4256. https://doi.org/10.1111/j.1365-294X.2012.05696.x

Shapiro, A. M. (1996). Status of butterflies. In *Sierra Nevada Ecosystem Project: Final report to congress*, 2 (pp. 743–757). University of California, Centers for Water and Wildland Resources. https://pubs.usgs.gov/dds/dds-43/VOL_II/VII_C27.PDF

Shreeve, T. G. (1992). Monitoring butterfly movements. In R. L. H. Dennis (Ed.), *The ecology of butterflies in Britain* (pp. 120–138). Oxford University Press.

Singer, M. C. (1972). Complex components of habitat suitability within a butterfly colony. *Science*, *176*(4030), 75–77. https://doi.org/10.1126/science.176.4030.75

Singer, M. C., & Ehrlich, P. R. (1979). Population dynamics of the checkerspot butterfly *Euphydryas editha*. *Fortschritte der Zoologie*, *25*, 53–60.

Singer, M. C., & Parmesan, C. (2018). Lethal trap created by adaptive evolutionary response to an exotic resource. *Nature*, *557*(7704), 238–241. https://doi.org/10.1038/s41586-018-0074-6

Singer, M. C., Ng, D., & Thomas, C. D. (1988). Heritability of oviposition preference and its relationship to offspring performance within a single insect population. *Evolution; International Journal of Organic Evolution*, *42*(5), 977–985. https://doi.org/10.1111/j.1558-5646.1988.tb02516.x

Singer, M. C., Thomas, C. D., & Parmesan, C. (1993). Rapid human-induced evolution of insect–host associations. *Nature*, *366*(6456), 681–683. https://doi.org/10.1038/366681a0

Sparks, T. H., & Yates, T. J. (1997). The effect of spring temperature on the appearance dates of British butterflies 1883–1993. *Ecography*, *20*(4), 368–374. https://doi.org/10.1111/j.1600-0587.1997.tb00381.x

Sperling, F. A. H., Sperling, W., & MacDonald, Z. G. (2020). Canadian Alpine butterflies deserve better monitoring. *State of the mountains report* (pp. 31–34). https://www.stateofthemountains.ca/s/ACC-SotM-2020-MAR22-2021.pdf

Sperling, F. A. H. (2003). Butterfly molecular systematics. In C. L. Boggs, W. B. Watt & P. R. Ehrlich (Eds.), *Butterflies: Ecology and evolution taking flight* (pp. 431–458). University of Chicago Press.

Steffan-Dewenter, I., & Tscharntke, T. (2000). Butterfly community structure in fragmented habitats. *Ecology Letters*, *3*(5), 449–456. https://doi.org/10.1111/j.1461-0248.2000.00175.x

Stefanescu, C., Páramo, F., Åkesson, S., Alarcón, M., Ávila, A., Brereton, T., Carnicer, J., Cassar, L. F., Fox, R., Heliölä, J., Hill, J. K., Hirneisen, N., Kjellén, N., Kühn, E., Kuussaari, M., Leskinen, M., Liechti, F., Musche, M., Regan, E. C., . . . & Chapman, J. W. (2013). Multi-generational long-distance migration of insects: Studying the painted lady butterfly in the western Palaearctic. *Ecography*, *36*(4), 474–486. https://doi.org/10.1111/j.1600-0587.2012.07738.x

Sweaney, N., Lindenmayer, D. B., & Driscoll, D. A. (2014). Is the matrix important to butterflies in fragmented landscapes? *Journal of Insect Conservation*, *18*(3), 283–294. https://doi.org/10.1007/s10841-014-9641-9

Tabarelli, M., Peres, C. A., & Melo, F. P. L. (2012). The “few winners and many losers” paradigm revisited: Emerging prospects for tropical forest biodiversity. *Biological Conservation*, *155*, 136–140. https://doi.org/10.1016/j.biocon.2012.06.020

Thomas, J. A. (1991). Rare species conservation: Case studies of European butterflies. In I. F. Spellerberg, F. B. Goldsmith & M. G. Morris (Eds.), *The scientific management of temperate communities for conservation* (pp. 149–197). Blackwell Scientific.

Thomas, J. A. (2005). Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *360*(1454), 339–357. https://doi.org/10.1098/rstb.2004.1585

Thomas, C. D., Singer, M. C., & Boughton, D. A. (1996). Catastrophic extinction of population sources in a butterfly metapopulation. *American Naturalist*, *148*(6), 957–975. https://doi.org/10.1086/285966

Thomas, J. A., Bourn, N. A. D., Clarke, R. T., Stewart, K. E., Simcox, D. J., Pearman, G. S., Curtis, R., & Goodger, B. (2001). The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proceedings. Biological Sciences*, *268*(1478), 1791–1796. https://doi.org/10.1098/rspb.2001.1693

Tilman, D., Clark, M., Williams, D. R., Kimmel, K., Polasky, S., & Packer, C. (2017). Future threats to biodiversity and pathways to their prevention. *Nature*, *546*(7656), 73–81. https://doi.org/10.1038/nature22900

UN Environmental Program. (2021). WCMC IUCN. *Protected planet: The world database on protected areas (WDPA)*. https://www.protectedplanet.net/en

Van Nouhuys, S., & Hanski, I. (2002). Colonization rates and distances of a host butterfly and two specific parasitoids in a fragmented landscape. *Journal of Animal Ecology*, 71(4), 639–650. https://doi.org/10.1046/j.1365-2656.2002.00627.x

van Swaay, C., & Warren, M. (1999). *Red data book of European butterflies (Rhopalocera)*. Council of Europe.

van Swaay, C., Warren, M., & Loïs, G. (2006). Biotope use and trends of European butterflies. *Journal of Insect Conservation*, *10*(2), 189–209. https://doi.org/10.1007/s10841-006-6293-4

van Swaay, C., Maes, D., Collins, S., Munguira, M. L., Šašić, M., Settele, J., Verovnik, R., Warren, M., Wiemers, M., Wynhoff, I., & Cuttelod, A. (2011). Applying IUCN criteria to invertebrates: How red is the Red List of European butterflies? *Biological Conservation*, *144*(1), 470–478. https://doi.org/10.1016/j.biocon.2010.09.034

Vera, F. W. M. (2000). *Grazing ecology and forest history*. CABI.

Wallace, A. R. (1865). I. On the phenomena of variation and geographical distribution as illustrated by the Papilionidae of the Malayan Region. *Transactions of the Linnean Society of London*, *25*(1), 1–71. https://doi.org/10.1111/j.1096-3642.1865.tb00178.x

Wallis DeVries, M. F. (2004). A quantitative conservation approach for the endangered butterfly *Maculinea alcon*. *Conservation Biology*, *18*(2), 489–499.

Wang, T., Hamann, A., Spittlehouse, D., & Carroll, C. (2016). Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLOS ONE*, *11*(6), e0156720. https://doi.org/10.1371/journal.pone.0156720

Warren, M. S., Hill, J. K., Thomas, J. A., Asher, J., Fox, R., Huntley, B., Roy, D. B., Telfer, M. G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S. G., Greatorex-Davies, J. N., Moss, D., & Thomas, C. D. (2001). Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, *414*(6859), 65–69. https://doi.org/10.1038/35102054

Watt, W. B. (2003). Mechanistic studies of butterfly adaptation. In C. L. Boggs, W. B. Watt & P. R. Ehrlich (Eds.), *Butterflies: Ecology and evolution taking flight* (pp. 319–352). University of Chicago Press.

Wenzel, M., Schmitt, T., Weitzel, M., & Seitz, A. (2006). The severe decline of butterflies on western German calcareous grasslands during the last 30 years: A conservation problem. *Biological Conservation*, *128*(4), 542–552. https://doi.org/10.1016/j.biocon.2005.10.022

Westwood, A. R., & Blair, D. (2010). Effect of regional climate warming on the phenology of butterflies in boreal forests in Manitoba, Canada. *Environmental Entomology*, *39*(4), 1122–1133. https://doi.org/10.1603/EN09143

Wettstein, W., & Schmid, B. (1999). Conservation of arthropod diversity in montane wetlands: Effect of altitude, habitat quality and habitat fragmentation on butterflies and grasshoppers. *Journal of Applied Ecology*, *36*(3), 363–373. https://doi.org/10.1046/j.1365-2664.1999.00404.x

White, R. P., Murray, S., & Rohweder, M. (2000). *Pilot assessment of global ecosystems: Grassland ecosystems*. World Resources Institute.

Wilcox, B. A., Murphy, D. D., Ehrlich, P. R., & Austin, G. T. (1986). Insular biogeography of the montane butterfly faunas in the Great Basin: Comparison with birds and mammals. *Oecologia*, *69*(2), 188–194. https://doi.org/10.1007/BF00377620

Wilson, E. O., & MacArthur, R. H. (1967). *The theory of island biogeography*. Princeton University Press.

Wissel, C., Stephan, T., & Zaschke, S.-H. (1994). Modelling extinction and survival of small populations. In H. Remmert (Ed.), *Minimum animal populations* (pp. 67–103). Springer. https://doi.org/10.1007/978-3-642-78214-5_6

Wood, B. C., & Pullin, A. S. (2002). Persistence of species in a fragmented urban landscape: The importance of dispersal ability and habitat availability for grassland butterflies. *Biodiversity and Conservation*, *11*(8), 1451–1468. https://doi.org/10.1023/A:1016223907962

Zschokke, S., Dolt, C., Rusterholz, H. P., Oggier, P., Braschler, B., Thommen, G. H., Lüdin, E., Erhardt, A., & Baur, B. (2000). Short-term responses of plants and invertebrates to experimental small-scale grassland fragmentation. *Oecologia*, *125*(4), 559–572. https://doi.org/10.1007/s004420000483