

Climate change effects on animal ecology: butterflies and moths as a case study

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ABSTRACT

Butterflies and moths (Lepidoptera) are one of the most studied, diverse, and widespread animal groups, making them an ideal model for climate change research. They are a particularly informative model for studying the effects of climate change on species ecology because they are ectotherms that thermoregulate with a suite of physiological, behavioural, and phenotypic traits. While some species have been negatively impacted by climatic disturbances, others have prospered, largely in accordance with their diversity in life-history traits. Here we take advantage of a large repertoire of studies on butterflies and moths to provide a review of the many ways in which climate change is impacting insects, animals, and ecosystems. By studying these climate-based impacts on ecological processes of Lepidoptera, we propose appropriate strategies for species conservation and habitat management broadly across animals.

Key words: asynchrony, butterfly, insect, morphology, moth, parasitoid, phenology, range shift, trophic mismatch, voltinism

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I. INTRODUCTION

Climate change is affecting ecosystems on all scales from individual genotypes to entire communities (Wilson & Maclean, 2011; Wymore *et al.*, 2011; Scheffers *et al.*, 2016; Cohen, Lajeunesse & Rohr, 2018). Despite a substantial body of literature, it is still difficult to predict ecological responses to climate change. Evidence is scattered across taxa, habitats, populations, and communities (Parmesan & Yohe, 2003; Parmesan, 2006; Merilä & Hendry, 2014; Lister & Garcia, 2018; Wepprich *et al.*, 2019), making it difficult to discern broad patterns in responses across time and space. Scheffers *et al.* (2016) provided a unifying synthesis of evidence on climate change impacts across the hierarchy of biological organization but to do so, the authors had to collate evidence from diverse taxa and ecological systems. Here we complement this approach with a deeper synthesis of a single, well-studied taxon to recommend best conservation and management practices for organisms with overlapping traits and ecologies.

Insects have been proposed as informative models for testing climate change impacts on ecological systems because they show rapid responses to changes in their environment due to short generation times and sensitive ecological requirements (Nadeau, Urban & Bridle 2017). There is mounting evidence that they are disappearing rapidly, with climate change being a major contributing factor (Oliver *et al.*, 2015; Forister, Pelton & Black, 2019; Soroye, Newbold & Kerr, 2020; Wagner, 2020; Halsch *et al.*, 2021). Understanding the effects of climate change on insects is therefore a top priority for conservationists, as they play an important role in shaping Earth's biota (Misof *et al.*, 2014), and make up the largest proportion of animal diversity and biomass (Bar-On, Phillips & Milo, 2018). Unfortunately, the life histories of many insect groups are not well understood. The one exception is the butterflies and moths (Lepidoptera), undoubtedly the best-studied insect lineage, and is already responding to climate change, habitat loss, and habitat fragmentation (Warren *et al.*, 2001; Wilson & Maclean, 2011; Fox, 2013; Belitz *et al.*, 2018; Maurer *et al.*, 2018; Ellis *et al.*, 2019).

Butterflies and moths are well suited as a model for uncovering patterns in the effects of climate change on ecosystems since the literature on this group demonstrates how organismal (genetics, physiology, behaviour, morphology), phenological (host synchrony, voltinism), population-level (geographic ranges), and community-level (trophic interactions e.g. parasitoid–herbivore) processes interact and respond to change. They are an ideal group for investigating associations between species traits and range shifts due to the availability of accurate scientific information on their biology, and the distributional data from citizen science monitoring schemes. Lepidoptera have proved useful in monitoring ecological and evolutionary responses to climate because they capture the diversity of responses across insects: (i) they

possess a suite of genetic, physiological, and morphological traits with known sensitivity to climatic variables. Several studies have recorded their capacity for rapid evolutionary change *via* genetic and phenotypic responses to current warming. (ii) They have complex life cycles that span a wide array of life-history strategies relating to development time, emergence time, foraging behaviour, survivorship, and voltinism. (iii) They exemplify the complexity of geographical responses to climate change – some species of Lepidoptera have undergone local extinctions, while others have experienced population increases.

To complement Scheffers *et al.* (2016), who summarized evidence across multiple taxa and systems, we focus on the extensively studied butterflies and moths to uncover systematic biological responses to climate change within a phylogenetically related but diverse group of organisms in a wide range of habitats and ecosystems. We use case studies from contemporary literature to identify and discuss climate change impacts on ecological processes (Fig. 1), determine research gaps, and propose future directions for climate change research. Our synthesis on a well-studied model taxon serves to illustrate many of the general trends purported in the ecological climate change literature.

II. ORGANISMAL RESPONSES

The most obvious impact of climate change is that species adapted to cooler environments will find it increasingly difficult to acclimate to warmer ones. In such circumstances, they may escape extinction by either adapting *in situ* to the warmer climate or moving to a cooler one, depending on the respective availability of genotypes that are heat-tolerant and/or predisposed to high dispersal. In this section, we discuss how these adaptive genotypes respond to climate change in Lepidoptera.

(1) Genetic

Genetic variation can allow a species to tolerate different environments when selection acts on dispersal capacity (Canale & Henry, 2010). The effects of anthropogenic climate change have already altered the selective pressures on butterfly populations, leading to allele frequency shifts associated with dispersal (Karl, Schmitt & Fischer, 2009; Kleckova & Klecka, 2016). Genetic polymorphisms in the *Pgi* gene encoding phosphoglucose isomerase have been shown to influence several key life-history traits in adult insects, including dispersal, flight metabolism, longevity, and fecundity (Watt, 1983; Saastamoinen, Ikonen & Hanski, 2009; Kallioniemi & Hanski, 2011). In butterflies, *Pgi* heterozygotes have increased fitness in cooler climates as they are capable of flying at lower ambient temperatures than their homozygote counterparts (Niitepõld *et al.*, 2009). Genetic variation in *Pgi* in the Glanville fritillary (*Melitaea cinxia*) directly affects

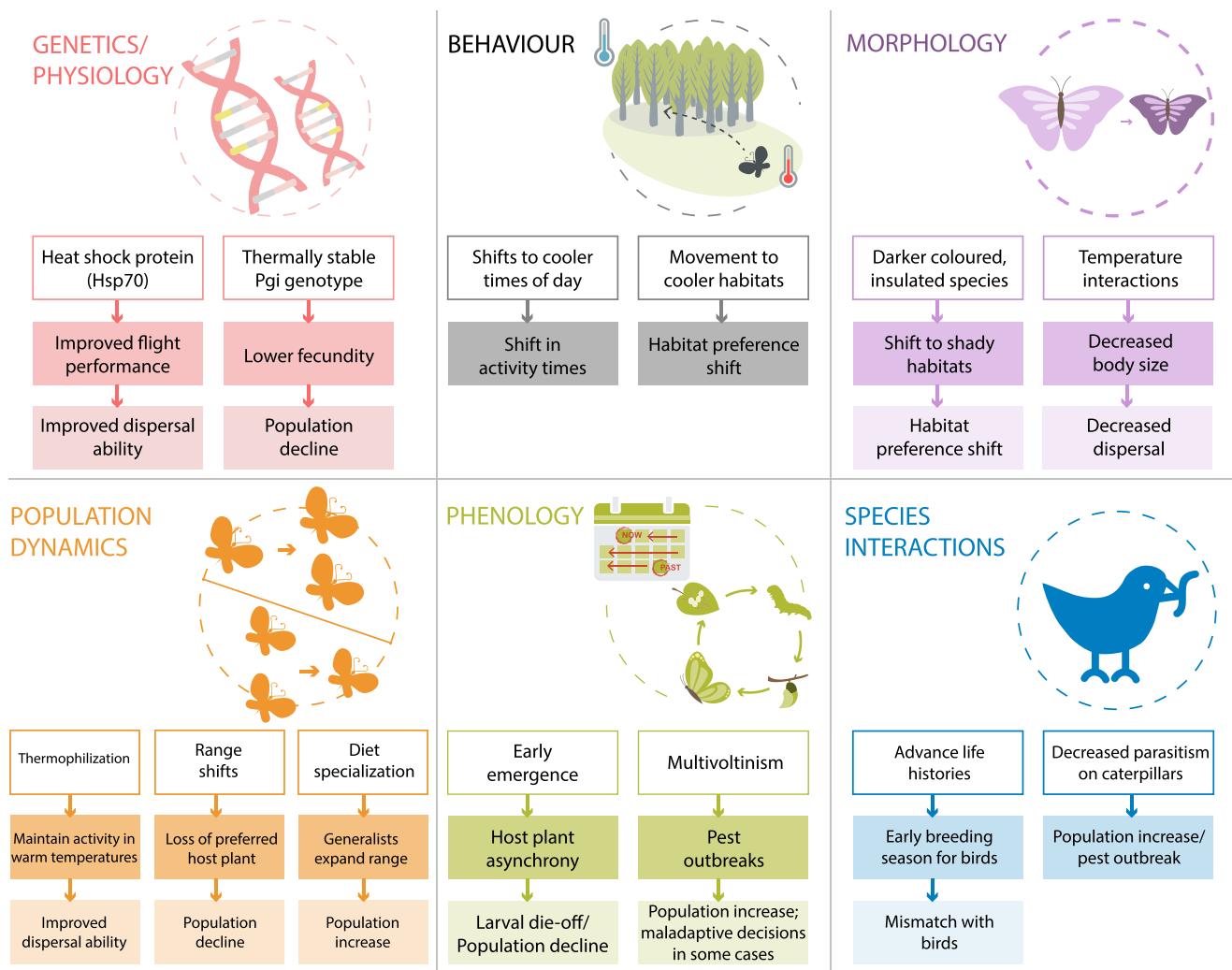


Fig 1. Examples of predicted and observed responses of Lepidoptera to climate change. Each response within the ecological processes has at least one supporting case study. Case studies include: Dewar & Watt (1992); Williams & Liebhold (1995); Parmesan *et al.* (1999); McLaughlin *et al.* (2002); Crozier (2003); Parmesan & Yohe (2003); Visser *et al.* (2004); Stireman *et al.* (2005); Wilson *et al.* (2005); Thomas (2005); Kiritani (2006); Parmesan (2006); Nogués-Bravo *et al.* (2007); Hellmann *et al.* (2008); Menéndez *et al.* (2008); Schweiger *et al.* (2008); Dukes *et al.* (2009); Pelini *et al.* (2009); Altermatt (2010a); Singer & Parmesan (2010); Chen *et al.* (2011); Finkbeiner *et al.* (2011); Betzholtz *et al.* (2012); Breed *et al.* (2013); Bonebrake *et al.* (2014); Kingsolver & Buckley (2014); Aalberg Haugen & Gotthard (2015); Duque *et al.* (2015); Filz & Schmitt (2015); Van Dyck *et al.* (2015); Chuang & Peterson (2016); Kleckova & Klecka (2016); Melero *et al.* (2016); Molina-Martínez *et al.* (2016). *Pgi*, phosphoglucose isomerase.

dispersal rates and metapopulation dynamics (Haag *et al.*, 2005; Hanski & Saccheri, 2006; Saastamoinen & Hanski, 2008). Similarly, in the map butterfly (*Araschnia levana*), individuals have higher levels of dispersive *Pgi* alleles at newly colonized sites, even though these individuals appear to have no morphological changes that improve flight performance such as increased wing or thorax size (Mitikka & Hanski, 2010). These results suggest that range expansions may be assisted by, or even dependent on, the selection of dispersive *Pgi* alleles in thermally challenged species.

Pgi alleles are also associated with heat resistance in Lepidoptera, but selection of resistant genotypes in warmer

environments may be impeded by trade-offs with other important life-history traits. In *Colias* butterflies, the genotypes that are the most heat stable are also the least fecund, so selection for heat tolerance could greatly reduce population sizes (Watt, 1992). In general, *Pgi* genotypes that are associated with a narrow window of flight are more metabolically active, more fecund, and less heat resistant, whereas genotypes associated with a broad flight window have lower kinetic power, lower fecundity, and increased resistance to heat (Schneider & Root, 2002). Selection for heat-resistant *Pgi* alleles under global warming may therefore be hampered by associated costs of decreased fecundity and reduced

dispersal; however, *Pgi* is not directly influential in heat resistance in *Lycaena tityrus* (Fischer & Karl, 2010), so trade-offs may vary among taxa. Future studies on the role of *Pgi* could be extremely important for conservation genetics, since it can be used to detect local adaptation and dispersal in changing environments (Wheat, 2010).

Another molecular marker that is likely to be important in the response to climate change is the heat shock protein (Hsp70). Hsp70 genes play a critical role in helping insects survive exposure to extreme temperatures by increasing heat tolerance (Wang *et al.*, 2015). Under normal conditions, Hsp70 is expressed at very low levels, but expression increases quickly in response to extreme temperature-related stress (Bahar *et al.*, 2013). This response was observed in wide-ranging moth pests, including the diamondback moth (*Plutella xylostella*) and setaceous Hebrew character moth (*Xestia c-nigrum*) where the expression of several Hsp70 genes became more frequent when exposed to heat or cold stress (Bahar *et al.*, 2013; Yang *et al.*, 2015). Thus, sensitivity in gene expression of Hsp70 can be used to evaluate a species' ability to adjust to short-term extreme temperatures (Bahar *et al.*, 2013). Hsp70 genotypes are also associated with body temperature and metabolic rate prior to flight in *M. cincta* (Mattila, 2015), which might allow improved flight performance under higher temperatures in the future. Taken together, *Pgi* and *Hsp70* offer a robust comparison of key genes and phenotypes that are directly impacted by a changing climate. Although further genetic markers have been uncovered in other animals and plants (Hoffmann & Daborn, 2007; Franks, Weber & Aitken, 2014), markers need to be established for species from broader phylogenetic and ecological contexts (Varshney *et al.*, 2018). The utility of *Pgi* and *Hsp70* suggests that genes associated with thermoregulation and dispersal may be highly informative and would be a useful target in future research.

(2) Behavioural

Behavioural plasticity is especially important for ectotherms like butterflies and moths which must seek out the correct environment to keep their body temperature at an optimum (behavioural adaptations). For example, species living in alpine habitats hold their wings perpendicular to the sun (basking) while at rest to increase exposure to heat (Kingsolver, 1985). Conversely, those in warmer climates adopt a heat-avoidance posture, like *Chlosyne lacinia* and *Colias* butterflies, which inhabit open habitats and orient away from the sun to avoid reaching lethal body temperatures (Bonebrake *et al.*, 2014; Kingsolver & Buckley, 2014). In response to increasing temperatures and sunlight, heat avoidance and basking behaviours are likely to become more and less frequent, respectively. Species that exhibit avoidance behaviours could have a selective advantage in open, exposed environments where direct sunlight may push individuals towards their lethal limits (Bonebrake *et al.*, 2014) but may also face context-dependent challenges if posturing impacts camouflage or foraging time.

Seeking optimal microhabitats is likely to be the most common behavioural response of butterflies and moths to climate change. Species residing in cool habitats may take advantage of warmer microclimates to enhance their body temperature, while species in warmer habitats, such as those at lower elevations, may retreat to cooler, more shaded microhabitats (Kleckova & Klecka, 2016). For instance, larvae of the two swallowtail butterflies, the Apollo butterfly (*Parnassius apollo*) and pipevine swallowtail (*Battus philenor*) move between microhabitats depending on ambient temperature and sunlight (Nice & Fordyce, 2006; Ashton, Gutiérrez & Wilson, 2009). *P. apollo* larvae spend time thermoregulating in areas with reduced vegetation cover at higher, cooler elevations, whereas at lower, warmer elevations, they spend more time in sheltered, shady areas (Ashton *et al.*, 2009). Caterpillars of the small eggar (*Eriogaster lanestris*) can reach their thermal optimum over a wide range of ambient temperatures by changing position within their layered, silken tents (Ruf & Fiedler, 2002). These examples suggest that climate warming may trigger widespread changes in microhabitat preference and increased microhabitat-seeking behaviours. Species that exhibit a greater capacity for thermoregulatory behaviour may be the best suited to meet changes in temperature and solar radiation (cloud cover). Furthermore, the success of optimal habitat-seeking will depend on other factors, such as the existing thermal requirements of a species, and whether optimal microhabitats are available (Kleckova & Klecka, 2016).

Sociality is another trait that has been associated with a species' tolerance to external temperatures, suggesting that social behaviours may become a selective advantage as global temperatures continue to change. A comparative study between two gregarious and two solitary moth species showed that gregarious larvae had a greater ability to adjust their body temperatures, while solitary species were more dependent on external temperatures (Bryant, Thomas & Bale, 2000). The thermoregulatory behaviour of tent caterpillars may also be linked to their gregarious nature (Ruf & Fiedler, 2002). With only a few examples, it is difficult to suggest whether this is a general trend, but this is an important area for future research.

The consequences of climate change will also depend on how well thermoregulatory behaviours synchronize with changing seasonal activity and reproduction, and how shade availability is affected by changes in vegetation cover (Kearney, Shine & Porter, 2009). Increased temperatures in certain environments may limit activity time and increase maintenance energy costs, such as those associated with seeking optimal microhabitats (Kearney *et al.*, 2009). Additionally, microclimate has impacts on the phenology of host plants and nectar sources, which can in turn affect behaviour, such as in Edith's checkerspot (*Euphydryas editha*) caterpillars which disperse towards optimal microhabitats and host plants (Weiss, Murphy & White, 1988). These examples highlight the importance of incorporating information on behaviours such as microhabitat and host seeking into life-history studies. Ecological characterizations are still sorely

lacking across the tree of life, with 88–95% of eukaryotes still undescribed (Mora *et al.*, 2011; Hawksworth & Lücking, 2017; Stork, 2018). Habitat and temperature requirements of under-represented taxa, and the behavioural mechanisms used to maintain those requirements, are critical research areas to inform conservation strategies under climate change.

(3) Morphological

Morphological responses to climate change are some of the best documented, largely because of specimen records in natural history collections (e.g. MacLean *et al.*, 2018). Several studies have demonstrated how decreased melanism and variable colour patterns may provide selective advantages in rising temperatures (Forsman, Betzholtz & Franzén, 2016; Scriber, 2020). Darker, more melanic wings allow butterflies to absorb more heat in cooler microclimates, and longer setae on the thorax help to retain heat and increase body temperatures at higher elevations (Kingsolver & Moffat, 1982). Phenotypic plasticity of these traits provides an adaptive route for a species to thermoregulate according to changing temperatures. For example, *Colias meadii* butterflies subjected to colder temperatures during pupal development have increased wing melanism and longer setae at high elevations (MacLean, Kingsolver & Buckley, 2016). Plasticity in larval colour pattern can also provide adaptive resilience. In the pipevine swallowtail (*B. philenor*), a greater proportion of red larvae are produced at warmer temperatures, and a black phenotype is maintained at cooler temperatures, allowing them to cope better with critical thermal extremes (Nice & Fordyce, 2006). For some European butterflies, dark-coloured and lighter-coloured individuals are selected in cooler and warmer climates, respectively (Zeuss *et al.*, 2014). When temperatures are high, light-coloured species can be active for longer periods during the day than dark-coloured species, which broadens the range of suitable habitats at low latitudes. A similar trend is found in Australian butterflies but at much smaller spatial scales. Here, darker and larger butterflies preferred cool, shady habitats since they absorb heat faster compared to lighter-coloured and smaller butterflies (Xing *et al.*, 2016). Thus, climate warming may present new fitness costs or trigger habitat shifts, with darker coloured species shifting their behaviour and preference towards more shady habitats, shorter activity times and cooler regions, which might represent a last-resort climate change refuge, after which localized extinctions of dark species might occur.

Near-infrared reflectivity of some butterfly wings helps to control heat gain and may be selected for under climate change as temperatures increase (Munro *et al.*, 2019). In general, heat-avoidance morphologies such as reflectivity and reduced melanism will present an advantage for butterflies in warming climates, while plasticity or high intraspecific variation of any thermoregulatory morphology is likely to provide resilience in fluctuating environments prone to extreme weather events, which are predicted to occur more

frequently under climate change. For example, species with more variable colour patterns may have an advantage over monotypic species (Forsman *et al.*, 2016). However, some trade-offs can be expected for traits like melanism, which also confer functions associated with immune responses or life histories (Clusella-Trullas & Nielsen, 2020).

Intuitively, one might expect that largely nocturnal species may not benefit from either behavioural thermoregulatory modifications or melanism in response to climate exposure. Yet, Xing *et al.* (2018) show that geometrid moths, which are primarily nocturnal in activity, show disproportionately darker moth species at high elevations. Their result suggests that the distribution of colour lightness of nocturnal moths is affected by temperature and solar radiation, especially along climatically harsh environmental gradients where organisms are under strong selective pressures. An interesting topic for future research would therefore be to investigate the importance of dark colour patterns for the thermoregulatory activity and UV protection of night-flying moths.

The effect of climate change on lepidopteran body size is more difficult to predict, with studies showing differing responses depending on phenology and existing plasticity. Across ectotherm taxa, warming global temperatures often appear to result in smaller body size (Ohlberger, 2013; Coulthard *et al.*, 2019) by shortening development time (Sheridan & Bickford, 2011). Larger bodies have also been shown to reduce the time needed to raise body temperature for flight activity in cold environments (Nève & Després, 2020), an adaptation that may not confer the same advantages with increasing temperatures. In the Arctic butterflies *Boloria chariclea* and *Colias hecla*, decreases in body and wing size were observed in response to 17 years of rising summer temperatures in Greenland (Bowden *et al.*, 2015). However, recent work suggests that the effect of temperature on body size in insects can be more complex and varied. For example, increased wing length is correlated with warmer temperatures during specific pupal periods in *Anthocharis cardamines* butterflies (Davies, 2019). The impact of temperatures experienced during development on adult body size in butterflies has also been analysed in museum specimens of *Hesperia comma* (Fenberg *et al.*, 2016), *Polyommatus argus*, *Polyommatus bellargus* and *Polyommatus coridon* (Wilson, Brooks & Fenberg, 2019). The direction (increased or decreased wing length) of the response to temperature varied with developmental stage, sex, and generation, suggesting that complex ecological and evolutionary feedbacks within populations may be triggered by climate change.

Climate change, and warming temperature especially, can cause conflict between morphological traits like body and wing size, and ecological traits like dispersal. In cases where changing climates cause decreases in body size, a major consequence is reduced dispersal capacity and fecundity. Morphometric data from the swallowtail butterfly (*Papilio machaon britannicus*) show that, as populations contracted over time in England, selection against dispersal from isolated habitats led to morphological changes associated with decreased body size (Dempster, King & Lakhani, 1976).

The converse of this process, whereby selection for reduced body size in warmer environments leads to associated loss of dispersal capacity, may therefore be expected under climate change. In Bornean geometrid moths, a reduction in wing size at high altitudes was tied to uphill range shifts of smaller species after four decades of warming (Wu *et al.*, 2019); unequal redistribution of different sized species under climate change may therefore affect community size composition. In other cases, the effect on dispersal may be sex specific. The speckled wood butterfly (*Pararge aegeria*) generally has populations with larger adults and increased thorax size at newly colonized sites, but these phenotypic and evolutionary changes are more apparent in females than males which may impact responses to climate change (Hill, Thomas & Blakeley, 1999a; Hughes, Dytham & Hill, 2007). There is evidence that dispersal ability is not always associated with changes in body and wing size. Finnish populations of *M. cinxia* have increased dispersal ability in newly colonized sites, but do not exhibit any changes in flight morphology (Hanski *et al.*, 2002). However, Kuussaari, Nieminen & Hanski (1996) found that migratory female *M. cinxia* were larger (as measured by forewing length) than non-migratory individuals, and Davies & Saccheri (2013) found that smaller (wing-length) male *A. cardamines* were less dispersive in a localized English population than larger ones. Hence, the traits associated with dispersal may be cryptic (genetic, physiological, behavioural) or non-cryptic (morphological), and these may vary among populations and species. Because high dispersal rates are a distinguishing feature of species living in rapidly changing environments (Hanski, Saastamoinen & Ovaskainen, 2006), future research focusing on dispersal-linked morphological traits should yield promising results on range boundary expansion and colonization of novel habitats.

III. POPULATION-LEVEL RESPONSES

(1) Population and range expansion

The rate at which individual species shift their range is dependent upon multiple internal traits and external drivers. Range redistributions in butterflies and moths, such as those observed across Europe, Asia, and North America, have been associated with ecological generalization, dispersal ability and reproductive rate (Crozier, 2003; Kiritani, 2006; Parmesan, 2006; Dukes *et al.*, 2009; Pöyry *et al.*, 2009; Forister *et al.*, 2010; Breed, Stichter & Crone, 2013). For example, the sachem (*Atalopedes campestris*) is a coastal skipper butterfly with tropical origins formerly confined to the southwestern USA due to winter temperatures. Over the past 40 years, *A. campestris* has expanded its range northward up the west coast in response to warmer winters (Crozier, 2003). This species has been able to expand its range because it is not habitat or dispersal limited (Crozier, 2003). Thermophilization of communities is expected to occur across temperate,

boreal and arctic ecosystems as a result of warm-adapted species being favoured under climate change (Gottfried *et al.*, 2012; Duque, Stevenson & Feeley, 2015). Shifting ranges have already been observed for species in several butterfly families: Hesperiidae (propertius duskywing *Erynnis propertius*), Lycaenidae (brown argus *Aricia agestis*), Nymphalidae (speckled wood butterfly *P. aegeria*), and Papilionidae (giant swallowtail *Papilio cresphontes*, anise swallowtail *P. zelicaon*) (Hellmann *et al.*, 2008; Menéndez *et al.*, 2008; Finkbeiner *et al.*, 2011; Breed *et al.*, 2013), as well as agricultural and forest moth pest species like the African maize stalk borer (*Busseola fusca*) and the pine processionary moth (*Thaumetopoea pityocampa*) (Battisti *et al.*, 2005; Assefa *et al.*, 2015). These species can maintain activity during warm conditions and therefore have relatively longer flight periods, which can elevate dispersal rates (Zera & Denno, 1997). Population expansion appears to be more likely for winged ectotherms such as lepidopterans (Cudmore *et al.*, 2010; Mason *et al.*, 2019), compared to apterous endothermic species (Zhu, Woodall & Clark, 2012). In some instances, lepidopteran populations are performing better than expected (Hunter *et al.*, 2014), especially in complex ecological systems such as those in the tropics (Cheng *et al.*, 2019).

Diet specialization is a costly life-history strategy under a changing climate, since specialists are less likely to find suitable habitat patches during range shifts. There are a few cases of range expansion in specialists when their diets consist of high-nitrogen resources (Betzoltz *et al.*, 2012). In most cases, oligo- or polyphagous species (diet generalists) have an advantage because they have a wider breadth of host plants, allowing for easy colonization of new sites during range expansion (Betzoltz *et al.*, 2012). By contrast, diet and habitat specialists typically have poor dispersal ability and may not be able to track environmental changes when suitable habitat patches are reduced and fragmented, resulting in local extinctions and range declines (Warren *et al.*, 2001).

(2) Population and range retraction

While poleward expansions due to climate change are well documented in the literature, there is also evidence for population declines and local extinctions, especially for species with ranges that are limited by elevation. A survey of four butterfly species at 421 sites in the northern mountains of the UK showed that future climate warming jeopardizes the survival of all the species examined (Franco *et al.*, 2006). Montane species are especially vulnerable to climate change impacts because mountains are predicted to be subjected to extreme temperature increases (Nogués-Bravo *et al.*, 2007; Molina-Martínez *et al.*, 2016) and because altitudinal shifts of low-elevation species at range boundaries may confine them to more fragmented habitats (Wilson *et al.*, 2005). However, if cooler microclimates are available at higher elevations, cold-adapted species could remain in their optimal thermal window by shifting their range altitudinally rather than latitudinally (Beckage *et al.*, 2008). Since elevational

temperature gradients in tropical regions have a stronger effect on species' distributions than latitudinal gradients (Colwell *et al.*, 2008), with some exceptions (Braby *et al.*, 2014), it is likely that tropical organisms will respond to increasing temperatures with uphill shifts (Pounds, Fogden & Campbell, 1999; Colwell *et al.*, 2008; Chen *et al.*, 2011; Laurance *et al.*, 2011; Molina-Martínez *et al.*, 2016). In a study in Oaxaca, Mexico, tropical butterfly species occurring above 1000 m showed more marked changes in their elevational distribution compared to lower altitude species (Wilson *et al.*, 2005). Alpine ecosystems are one of the most threatened habitats under climate change. Invasive species are shifting further into these habitats and may have severe impacts on lepidopteran richness and species composition at local and regional scales (Bilá *et al.*, 2016).

In North America, Edith's checkerspot (*E. editha*) provides one of the best-documented cases of population-level extinctions (Thomas, Franco & Hill, 2006). Extinctions of two populations of *E. editha* were caused by both habitat loss and regional climate change, including increasing variability in precipitation (McLaughlin *et al.*, 2002). The West Virginia white butterfly (*Pieris virginiensis*) faces critical habitat loss due to climate change and is threatened by the introduction of the non-native herb *Alliaria petiolata*, on which it lays two-thirds of its eggs despite its unsuitability as a host plant (Davis *et al.*, 2016). In the UK, fine-resolution (1 km²) mapping demonstrated extinction gradients for three of four northern butterfly species, a lycaenid (*Aricia artaxerxes*) and two nymphalid species, *Erebia aethiops* and *E. epiphron* (Franco *et al.*, 2006). Although several studies have predicted and observed range retractions under climate change, further research is needed to assess impacts on individual populations since different species are likely to respond in individual ways to climate change, and new species associations will develop as climate warming continues (Huntley *et al.*, 1995; Hill, Thomas & Huntley, 1999b).

IV. PHENOLOGICAL RESPONSES

(1) Voltnism

With climate change altering the timing and characteristics of seasons worldwide, adaptation will be required for many species that express different traits during different times of the year, e.g. wet- and dry-season forms of multigenerational butterflies. Numerous butterfly and moth species have shifted their seasonal activities in response to variation in climatic patterns due to climate change (Pelini *et al.*, 2009). These shifts are linked to environmental suitability since many species generally have a restricted time period in the year in which to reproduce under favourable conditions (Chuang & Peterson, 2016). The number of generations per year (voltnism) can be critical for survival of a species because an additional generation per unit time may accelerate population growth (Altermatt, 2010a). Many species have more than

one brood per year (multivoltine), and can express two developmental pathways: accelerated growth or diapause that delays development until environmental conditions are suitable (typical in temperate insects to survive the winter) (Altermatt, 2010a). Multivoltine species are more likely to be successful under warmer temperatures. In northern European moth communities, increased multivoltinism has been observed in response to increased temperatures in the spring and summer months (Pöyry *et al.*, 2011). The benefit of multivoltinism may be even greater when phenological changes occur earlier. In a study of 130 British moths and butterflies, multivoltine species exhibited population increases and range expansions over 19 years, while univoltine species exhibited the opposite trends (Macgregor *et al.*, 2019a).

In many cases, climate change-mediated shifts in voltnism are associated with species' life cycles and larval diet spectrum (Altermatt, 2010b). For example, a study spanning 150 years on 566 European moth and butterfly species showed that, in response to climate change, species that fed on herbaceous plants demonstrated increased voltnism but smaller shifts in flight periods compared to species feeding on woody plants (Altermatt, 2010b). Multivoltinism has also been linked to pest outbreaks and could have consequences on agriculture and forestry (Altermatt, 2010a). The codling moth, *Cydia pomonella*, is a global pest in apple fruit production. In response to higher temperatures early in the year, it is able to increase its voltnism by adding an additional generation (El Iraqui & Hmimina, 2016).

When responding to climate change, shifts towards bi- or multivoltinism may not always be beneficial. Some butterflies or moths that reproduce multiple times per year may be more susceptible to climate change if the negative effects accumulate over several generations. In one study monitoring 82 butterfly species in the Mediterranean throughout the year, multivoltine species had the highest population fluctuations within seasons, and suffered population declines due to extreme drought events during late-summer generations (Melero, Stefanescu & Pino, 2016). Rapid environmental changes may also distort environmental cues that species use to time developmental decisions before winter. Species that reproduce multiple times per year use locally adapted photoperiod cues (Lindestad *et al.*, 2019), and have strong thermal plasticity may be particularly vulnerable to developmental traps (Van Dyck *et al.*, 2015). Overall fitness may be greatly reduced if developmental synchrony associated with multivoltinism and host plant phenology is disrupted (Altermatt, 2010a). Local populations and species interactions are expected to be significantly impacted by these phenological changes (Altermatt, 2010b; Forrest, 2016).

(2) Early emergence and asynchronies

Temporal mismatches with food resources is a major concern under climate change, and species will likely vary in their responses. Within Lepidoptera, differences in the magnitude of phenological shifts are correlated with various life-history

traits, including seasonal appearance, overwintering stage (diapause), food availability, habitat, altitude, and latitude (Altermatt, 2010a, 2012; Diamond *et al.*, 2011; Karlsson, 2014; Navarro-Cano *et al.*, 2015). Temperature increases alter the development of insect herbivores more than their hosts, leading to insect–plant asynchronies (Dewar & Watt, 1992; Pelini *et al.*, 2009). However, temperature is not the sole driver of phenological mismatch – increased variability in precipitation may also lead to population declines due to the timing of plant senescence relative to larval development (McLaughlin *et al.*, 2002). Many butterfly species have been recorded emerging earlier from diapause due to advanced springs, which may lead to larval die-off from subsequent returns to winter conditions or insufficient resources from slower host-plant responses (e.g. flowering phenology) (Sparks, Roy & Dennis, 2005; Parmesan, 2007). Species that overwinter in the pupal stage typically advance their phenology more than species that overwinter in the larval or egg stage (Altermatt, 2010a; Diamond *et al.*, 2011; Karlsson, 2014), indicating that species with overwintering pupae may be at greatest risk of climate change-related extinctions.

Indirect effects of fluctuating climates may also lead to asynchrony. Timing of snowmelt is an important trigger for alpine and temperate species to end diapause and influences population growth. For example, in Greenland, the dynamics of snowmelt and increased temperatures were correlated with the timing of onset, and the peak and end of the flight season of the Arctic butterflies *B. chariclea* and *C. hecla* (Høye *et al.*, 2014). Similarly, early spring snow melt from increased temperatures impacts the population dynamics of the Mormon fritillary (*Speyeria mormonia*) through direct effects on floral abundance impacting nectar availability, leading to decreased fecundity and offspring survival as larvae and pupae in the subsequent season (Boggs & Inouye, 2012).

Butterflies and moths are significantly affected by the availability and quality of host plants as they shift geographically due to warming temperatures (Pelini *et al.*, 2010). Unsynchronized geographic shifts between lepidopterans and their host plants may occur during climate change since they tend to disperse at different rates (Schweiger *et al.*, 2008; Pelini *et al.*, 2010; Posledovich *et al.*, 2018). Thus, unequal changes in the distribution of butterflies and moths and their host plants can cause mismatches and prevent butterfly and moth populations from establishing in new areas (Pelini *et al.*, 2010; Altermatt, 2010b, 2012; Diamond *et al.*, 2011; Karlsson, 2014; Navarro-Cano *et al.*, 2015).

Phenological plasticity has been observed in many species and is considered an indicator of resilience to climate change impacts. The species that are capable of shifting their phenology may be more successful than those that are not as adaptable (Willis *et al.*, 2010; Cleland *et al.*, 2012; Polgar *et al.*, 2013). For instance, lycaenid butterflies in the north-eastern USA are responding to climate change by flying earlier in warmer years (Polgar *et al.*, 2013). The orange tip butterfly (*A. cardamines*) in the Netherlands has advanced its first appearance in response to earlier warmer temperatures

in the spring (Van Der Kolk, Wallis DeVries & Van Vliet, 2016). This species has large latitudinal variation in host use, allowing it to mediate climate change by switching among plant species based on their flowering phenology (Van Der Kolk *et al.*, 2016) since the larvae feed on developing seed pods (Dempster, 1997). In general, species that feed on particular phenological (i.e. developmental) stages of their host plants (flower buds, young fruits, seeds, or young leaves) – termed phenological specialists (Navarro-Cano *et al.*, 2015; Stålhandske *et al.*, 2016) – may be buffered against phenological mismatches if they are also host generalists (Navarro-Cano *et al.*, 2015). However, phenological specialization could present challenges for host specialists since they cannot adjust for phenological mismatches by switching hosts (Navarro-Cano *et al.*, 2015; Davies, 2019). Further research is needed on individual lepidopteran species and their host preferences, especially along latitudinal gradients, to understand fully how species interactions are impacted by climate change (Navarro-Cano *et al.*, 2015). Additionally, future research should focus on recent shifts and adaptive evolution of host plants due to global warming, since relatively little is known about this (Macel *et al.*, 2017).

V. COMMUNITY RESPONSES (SPECIES INTERACTIONS)

(1) Trophic mismatches

The impacts of climate change on multi-trophic interactions are the most complex and likely the most important responses to understand. A study by Macgregor *et al.* (2019b) found no link between changes in moth biomass and ecosystem, mean precipitation, temperature, or plant productivity, possibly indicating that biomass changes can be instead attributed to asynchronies between host plants and predators resulting from climatic variability. Decoupled interactions between butterflies, their resources, and their predators have been observed in response to climate change in several cases (Visser, Bath & Lambrechts, 2004; Stireman *et al.*, 2005). For example, Hunter *et al.* (2014) found that larval moths that fed on non-vascular plants were likely to show negative responses during projected climate changes. Another notable mismatch has been seen between an insectivorous bird, the great tit (*Parus major*), which feeds its offspring on winter moth (*Operophtera brumata*) and oak leaf roller (*Tortrix viridana*) caterpillars. Peak caterpillar biomass of these two species has advanced earlier in the season, so this bird species may need to breed earlier to align with peak caterpillar abundance, or find other available foods (Visser, Holleman & Gienapp, 2006). Since the populations of both these moths can cause serious pest outbreaks, their decoupling from an important regulatory predator may have serious economic consequences.

Variation in environmental and climatic conditions can also lead to rapid changes in lepidopteran–parasitoid synchrony (Singer & Parmesan, 2010). Based on a comparison

of 15 databases from geographically dispersed Lepidoptera rearing programs ranging from southern Canada to central Brazil, levels of parasitism in caterpillars decreased as climatic variability increased (Singer & Parmesan, 2010). This decrease in parasitism intensifies the frequency of lepidopteran larval outbreaks since parasitoids play a strong role in regulating insect herbivore populations, and climatic variability impairs the ability of parasitoids to track hosts (Stireman *et al.*, 2005). Escape from parasitism may be important in range shifts, as demonstrated in the brown argus butterfly (*A. agestis*). In newly colonized areas, this species has lower mortality from parasitoids (Menéndez *et al.*, 2008) which has contributed to its expansion northward in the UK over the last 30 years. Climate change could also affect parasitism *via* changes in behaviour. Larvae of the Glanville fritillary (*M. cinxia*) use solar radiation to outpace a braconid wasp parasitoid, *Cotesia melitaearum*. Warmer temperatures create asynchrony by enabling faster developmental rates in caterpillars than their parasitoids (Van Nouhuys & Lei, 2004). By understanding the role of environmental variability on species interactions, we thus can gain insight into how the effects of climate change could impact larger processes at community and ecosystem levels (Jamieson *et al.*, 2012).

It is evident that many species differ in their physiological tolerances to varying climatic patterns, which may lead to asynchrony between trophic levels (Parmesan, 2006; Schweiger *et al.*, 2008; Filz & Schmitt, 2015). Species that rely on specific obligate biotic interactions, such as mutualism and parasitism, are of highest concern. Over the last 20 years, the largest declines in European butterflies have been demonstrated in myrmecophilic species (Thomas, 2005). Many species of Lycaenidae depend on ants for survival (Pierce *et al.*, 2002) and environmental changes might result in severe asynchrony between the butterflies and their hosts. In particular, *Phengaris* butterflies depend on *Myrmica* ants for the survival of their offspring. A study that evaluated niche overlap and host specificity for *Phengaris* butterflies and *Myrmica* ants under climate change scenarios revealed that the butterflies should retain their connection to their hosts and maintain similar niche overlap over time (Filz & Schmitt, 2015). However, these butterflies are also threatened by severe habitat loss, and conservation management plans should include the host ants and their current and future niches (Filz & Schmitt, 2015), which may affect their resilience as mutualists (Rafferty, CaraDonna & Bronstein, 2015). Similar studies need to assess climate change impacts on other endangered lycaenid butterflies and their host ants.

VI. APPLYING THE LEPIDOPTERA CLIMATE CHANGE MODEL

In our review we identified general patterns in how animals may respond to climate change by using the well-studied

Lepidoptera as a model taxon. One of the most frequent conclusions within the Lepidoptera literature is that phenotypic plasticity allows species to cope with changing climate. Phenotypic plasticity in physiology, behaviour, and phenology across developmental stages, habitats, and phylogeny typically confers resilience to climate change in Lepidoptera. Similar patterns have been found in other plants and animals (Charmantier *et al.*, 2008; Nicotra *et al.*, 2010; Seebacher, White & Franklin, 2015), suggesting that this may be a good indicator of species resilience. However, we caution using this as a rule; there are instances where ecological specialization can be a benefit under specific circumstances (Duputié *et al.*, 2015; Oostra *et al.*, 2018).

It has repeatedly been shown that climate change is altering the distribution of lepidopteran populations, with population retraction and local extinction being the most common responses (Lenoir *et al.*, 2020). This phenomenon is also repeatedly found in non-lepidopteran taxa, including plants, invertebrates, and vertebrates spanning diverse terrestrial, freshwater, and marine ecosystems (Maclean & Wilson, 2011; Cahill *et al.*, 2013; Selwood, McGeoch & MacNally, 2015). These broad trends within and across taxa strengthen the need for an increased effort toward climate change mitigation, and increased research on conservation strategies. It is worth noting that increased research on species ecology carries conservation benefits in the context of habitat loss and fragmentation, which are causing extinctions regardless of climate change.

The race to save imperilled species is likely to depend on the implementation of conservation genetics in the context of species-specific ecological requirements. As discussed in Section II.1, *Pgi* and *Hsp70* have been used in Lepidoptera to detect responses to climate change; microsatellites, functional genes, and other markers have proved to be similarly useful in many plants and animals (Vandergast *et al.*, 2008; Aitken & Whitlock, 2013; Fordham *et al.*, 2014; Franks *et al.*, 2014). Further research is needed to identify markers from diverse phylogenetic groups. However, the efficacy of genetic markers will depend on whether specific ecological information is available: a thorough understanding of a species' temperature, behavioural, and habitat preferences must be considered in conjunction with predicted gene functionality in altered environments for conservation efforts under climate change. Since ecological specialists are often the most threatened, carefully targeted ecological research will be required to determine the best conservation approaches. It thus is critical to continue ecological monitoring alongside implementation of habitat conservation and climate change mitigation practices (Thomas, 2016).

The impacts of climate change on community interactions are usually the hardest to detect, yet are likely one of the most important topics to address. It is evident from research across butterflies and moths that climate change can lead to detrimental impacts associated with symbiont and resource asynchronies. A similar impact is also foreseen in other plant and animal communities, with cascading ecological and evolutionary effects that become increasingly difficult to predict (Winder & Schindler, 2004; Lavergne *et al.*, 2010; Warren &

Bradford, 2014; Classen *et al.*, 2015; Chidawanyika, Mudavanhu & Nyamukondiwa, 2019). Many of these studies identify ecological specialization and symbiont fidelity as risk factors for adapting to climate change. Future research should integrate symbionts and their interactions within communities into conservation strategies.

VII. CONCLUSIONS

- (1) We examined the impacts of climate change on butterflies and moths. The effects of climate change on lepidopterans include: selection on dispersal (e.g. *Pgi*) genotypes, up-regulation of thermoregulation (e.g. heat shock protein) genes, decreased melanism, reduced body size, increased dispersal, shifts between microhabitats and across altitude and latitude, habitat and host generalization, a shift towards multiple generations per year, and early emergence from diapause.
- (2) The impact of climate change on the genetics, physiology, behaviour, and morphology of insects is understudied. The limited research that has been conducted focuses on a few species. Future research should be expanded to include additional taxa that are ecologically and phylogenetically divergent, to understand the effects of climate change.
- (3) Many species are expanding polewards to escape warming temperatures. Thermophilization and diet specialization may impact this process by affecting their ability to invade new habitats. Future research should focus on individual populations since these are likely to show local adaptation and hence unique responses to climate change.
- (4) There is much research available on phenology in a climate change framework for Lepidoptera. The majority of studies report early emergence from diapause and increasing asynchrony with host plants. This may be particularly crucial for specialists that use only a particular part of a plant, or a particular stage in its life history, and are therefore phenologically constrained – such as lycaenid butterflies that specialize on flower buds or seeds. Other climatic changes such as early snow melt and shifts in precipitation patterns have led to lepidopteran population declines and local extinctions. Changes to voltinism are common, with numerous species increasing the number of generations per year. Future research should investigate how host preferences are likely to change in relation to predicted phenological shifts due to climate change.

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