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SPECIES TRAITS OF RELEVANCE FOR CLIMATE VULNERABILITY AND THE PREDICTION OF PHENOLOGICAL RESPONSES TO CLIMATE CHANGE

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ABSTRACT. In many ways, known and unknown, climate change will affect species' distributions, life cycles, phenologies, and ultimately survival. Lepidoptera are among the organisms that have been shown to be strongly impacted by climate change, and their conservation presents challenges that are both unique and unprecedented. Various studies have sought to determine what ecological and life traits of Lepidoptera influence species' responses to climate change, and here I review the few studies that evaluate such responses over a long period of time for a large number of species for common associations. Species with wider geographic distribution and less habitat specificity are generally considered less vulnerable to climate change, while those with opposite traits are deemed more vulnerable. The latter are more likely to change their phenology in response to climate change. Larval diet breadth and composition, overwintering stage, and adult activity period appear to be consistent predictors of changes in flight phenology. The knowledge of these traits for species of concern allows us to assess the implications of the possible phenological changes, and decide what can be done about those changes. Determining how phenological changes may affect current management or conservation practices and defining actions and priorities can be crucial for the success of a conservation plan.

Additional key words: climate change, conservation planning, Lepidoptera, flight phenology, ecological traits

Climate and land use changes are likely to be the biggest challenges faced by species in this century, and many studies have addressed responses of different taxa to climate change across the globe (see Parmesan and Yohe 2003 for a review). While habitat loss has been a leading threat, especially to Lepidoptera species (Cormont et al. 2012; Koh et al. 2004), climate change can exacerbate this and other threats and make species adjustment to new conditions critically time-sensitive (McLaughlin et al. 2002).

Lepidoptera are among the most studied insect taxa, and therefore have been the focus of many studies on responses to climate change (Boggs et al. 2003). In a 2011 review, Wilson and Maclean state that the majority of the studies dealing with climate change and declining biodiversity in insects between 2005 and 2009 dealt with Lepidoptera, showing them to be very sensitive to climate change. The dependence on multitrophic interactions in different life stages—with food plants, natural enemies, and mutualistic species such as ants—paired with short and complex life cycles will likely affect lepidopteran ecological and evolutionary responses to climate change (Kingsolver et al. 2011). In fact, studies have found that certain life history stages seem to be more affected by warming temperatures than others, resulting in different responses in phenology (Williams et al. 2012; references therein). The simultaneous or sequential dependence on a suite of requirements that may asynchronously respond to climate changes may account for a great deal of their vulnerability. Possible scenarios could include larval food plants succumbing to climate-related events such as drought or extreme precipitation, thus eliminating the synchrony necessary for the Lepidoptera species to survive, or a species having a climate-induced extra generation, but the food plant senescing early and the resource not being available for that extra generation. Several studies have already indicated disruption of trophic interactions related to changes in climate (Both et al. 2009, Brook 2009, Hellmann et al. 2012, Pelini et al. 2010). In addition to their complex life histories, specific habitat affiliations, and geographic isolation, local variation and regional specialization in populations of some species may also be a factor in the response of Lepidoptera to climate change (see figure 1 in Hellmann et al. 2012). Therefore, Lepidoptera conservation in the face of climate change presents challenges that are unprecedented (Aardema et al. 2011, Hellmann 2002).

There is evidence that certain traits may lead to a higher or lower level of general vulnerability in Lepidoptera. In a study of 23 threatened and 72 non-threatened butterfly species, Kotiaho et al. (2005) found that depending on dispersal ability, larval specificity, adult habitat breadth, and length of flight period, predictions could be made in relation to their risk of extinction. Threatened butterflies tend to have narrow niches, restricted resource distribution, short flight spans, and limited capacity for dispersal, being specialists in both larval resource requirements and adult habitat requirements. Species with wider geographic distribution and less habitat specificity are generally considered less vulnerable to climate change, while those with opposite traits are deemed more vulnerable (Altermatt 2010, Diamond et al. 2011, Heikkinen et al. 2010, Kotiaho et al. 2005, Urban et al.

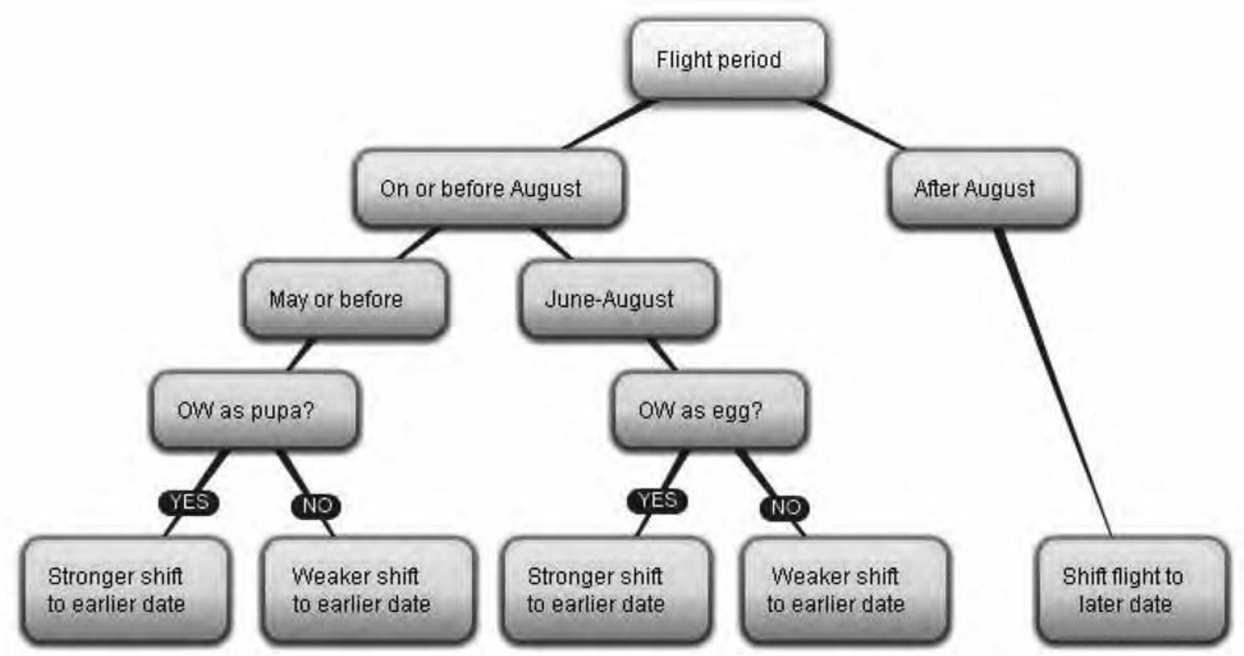

FIG. 1: Potential phenological responses based on adult flight period and overwintering stage. See text for description of studies used.

2012). A number of studies have shown that these characteristics have also been associated with a higher level of vulnerability specifically to climate change (Betzholtz & Franzen 2011, Franzén & Betzholtz 2012; but see Arribas et al. 2012). In addition to declines in numbers, that vulnerability may express itself in range shifts and phenological changes.

While many studies have sought to determine if species' range shifts can be attributed to climate change (e.g. Breed et al. 2012, Sunday et al. 2012), or how climate change will affect species range (Pelini et al. 2009), not many studies exist to date evaluating how traits influence phenological responses to climate change in large groups of Lepidoptera species. However, the few that do exist provide important results. Studies with large number of species over a long period of time carry special significance, since they can provide information on common responses across a number of species, which in turn can be applied to other species that share the characteristics or traits found to be either determinants or important variables in the species' ultimate response to climate changes.

This paper summarizes the traits associated with shifts in flight period to climate change, based on the existing multi-year, multispecies studies. The rationale for this exercise is that by knowing what a possible outcome will be, one can more effectively monitor and plan adaptation and conservation plans for various species of concern—those already threatened by climate change and those not yet affected.

MATERIALS AND METHODS

A 2012 literature search on the ISI Web of Science for the terms "Lepidoptera*" or "butterfl*" or "moth*" and "climate" or "warming" in the abstract and subject fields since 2000 yielded only eight studies done with traits of a large number of species over a significant period of time, and which could be construed as potentially predictive of responses to climate change for a variety of species. Of these, only five dealt with phenological responses. The studies evaluated from 95 to 556 species, over periods ranging from 3 to 150 years. The results of these five studies are summarized below with the use of diagrams instead of tables, for better visualization of responses. The results of other (not multi-species) studies are discussed in the ensuing section, when relevant.

All five studies were performed in Europe. Long term studies related to climate change are conspicuously lacking in North America, even though there are various long-term monitoring programs across the United States. Studies with fewer or single species from North America are mentioned in the discussion when relevant. There are differences in the species and

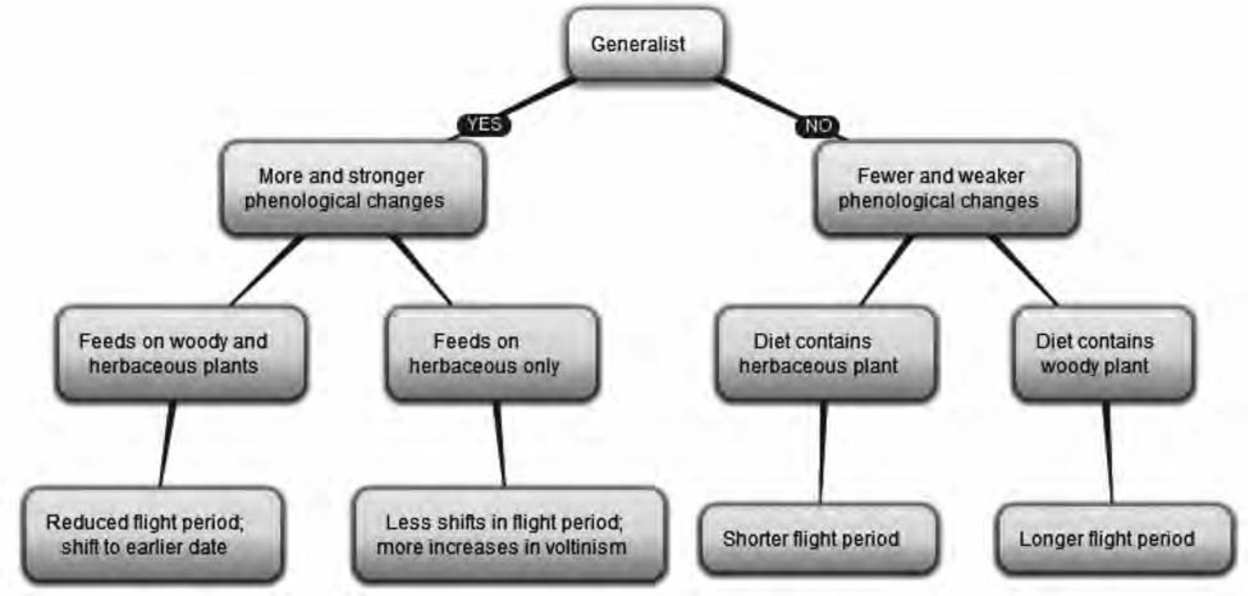

FIG. 2: Potential phenological responses based on larval diet breadth. See text for description of studies used.

habitats across the five studies, as well as land use patterns, but I focused on common responses of species independently of location. It is not the intent of this paper to list all possible or recorded responses of individual Lepidoptera species to climate change, nor the most important ones in an ecological, community, or population context. Instead, I focus on summarizing trait-based responses that have been found to be consistent for a group of species, across different studies and geographic locations. In the absence of other information for a species, the limited knowledge and the trends reported here could help identify possible responses of other species to climate change.

RESULTS

Flight period and overwintering stage are good predictors of flight phenology responses to climate change.

Three studies found significant relationships between flight period and overwintering stage and flight phenology in Lepidoptera, and these results are summarized in Figure 1.

Valtonen et al. (2011) analyzed flight times recorded at a network of sites in Finland over 12 years, and found that 51% of 112 study species had their phenology controlled by temperature, 1/3 of which were also influenced by photoperiod, while 24% were controlled by photoperiod alone. Species controlled by temperature alone (thermal control) should respond more readily in phenology to climate warming, and tend to be summer fliers (before August). That information is incorporated in the second branching of early flyers (“May or before” and “June–August”) in Figure 1.

Species in which photoperiod affects thermal controls —many spring fliers—may be slower in their response to climate change and are influenced by the overwintering stage. Those overwintering as pupae (and therefore ready to emerge as adults) tend to shift their activity period more strongly to an earlier date than those that overwinter as eggs or larvae (Valtonen et al. 2011). While the latter seem to be more affected by temperatures alone, their activity is delayed due to the further development they must go through before adults fly. It appears that summer flyers (June–August) tend to be less affected by temperature change, and overwintering stage is a better determinant of their phenological changes: while those that overwinter as eggs tend to accelerate their development with warmer temperatures and shift adult activity to an earlier date more markedly, those that overwinter as pupae do not respond as much to higher temperatures and tend to advance their phenology less. Altermatt (2010) also found that summer species that overwinter as eggs shifted more days (4) than do larvae (2) or pupae (1). He evaluated a 150-year dataset for 556 species of butterflies and moths in Central Europe and found in addition that species with median flight period before August shifted their flight period to an earlier date, while the ones with median flight period after August shifted to a later date.

Another study reports similar findings that support this framework. Using a long-term dataset from the U.K. Butterfly Monitoring Scheme, Diamond et al. (2011) found that overwintering stage was one of the significant predictors of phenological advancement in 44 species of butterflies over the past 30 years. The spring species that overwinter at more advanced stages tend to show more marked phenological advancement (May or before in Figure 1). They also found that species with earlier baseline dates of first appearance (earlier flight periods) expressed greater phenological advancement than those with a later flight period, probably due to exposure to greater mean increases in temperature (spring x summer) and also the fact that they tend to overwinter in later stages.

Feeding habit affects flight phenology responses to climate change.

Four studies found significant relationships between larval feeding habit and flight phenology in Lepidoptera, and those results are summarized in Figure 2.

Betzholtz & Franzen (2011) found that widely distributed generalist moths in Finland were more mobile than specialists with more restricted distributions. As stated above, being mobile can be an important factor in the species ability to track changes in climate. A generalist species can have the ability to use and also track various food plants as the latter change range, and use them effectively, while specialist or monophagous species are limited by the availability of their food plant. Generalist species have also long been associated with higher rates of dispersal, which can be a factor in their phenological responses to climate change. In general polyphagous and oligophagous species were more mobile than monophagous ones. Similar results were reported by Mattila et al. (2011) for Finnish butterflies: monophagous butterflies declined more in numbers than oligophagous or polyphagous ones, as did habitat specialists compared to intermediate and generalist species. More mobile species declined less than other categories. Monophagous species are less prone to leave their habitats, have more restricted distribution and therefore are more at risk from environmental changes.

Altermatt (2010) found that variation in phenological change was strongly related to traits describing plant-herbivore interactions (larval diet breadth, diet composition) and the life cycle. Species that included woody plants in their larval diet shifted more days to an earlier date on average than those that fed strictly on herbaceous plants, but the latter showed larger increases in voltinism (number of broods). Species whose larval diet included herbaceous plants with seasonal foliage showed the strongest trend toward a second generation, while species feeding on woody plants and herbaceous plants with year-round foliage showed the weakest shift in voltinism, similar to those species feeding on only herbaceous plants with year-round foliage. Species feeding on plants with year-round foliage, including woody plants, ranked between those 2 categories in terms of increased voltinism.

Interestingly, Diamond et al. (2011) found that species with narrower diet breadth experienced greater phenological advancement than those with a wider diet. This unexpected result could be associated with phenological advancement by a particular food plant, to which the specialist species would be responding (see Discussion section below).w

DISCUSSION

I used results of studies addressing species traits as possible determinants of phenological responses to climate change to show probable responses of Lepidoptera to warmer temperatures. While I expect this study to prove useful in designing conservation measures for butterflies and moths, especially in Europe, it is important to note that phenological responses to climate change are complex. According to Altermatt (2012), one cannot consider responses to climate change as a single-factor process. Rather, there are critical ecological and evolutionary constraints that affect species responses to climate change. Hellmann et al. (2012) mention ecological "surprises" that are likely to occur as a result of new interactions under climate change, and highlight the need for more studies on species interaction models and outcomes in order to design successful conservation management strategies.

If the expected outcome for a species does not occur, it is likely that an essential interaction has been affected by climate change also. So, when evaluating a possible response of a species to climate change, it is essential to also evaluate the responses of its food plant(s) and how those can affect the species' dynamics. In one example, Diamond et al. (2011) found that butterfly species in the U.K. with a narrow diet breadth actually showed greater phenological advancement, a response opposite to the predicted one. The authors hypothesize that such response may be have been enabled by a phenological advancement in one of the host plants. While species that depend on a few host plants have to be able to track climatic changes, species with a broader diet might not express phenological advancement if a few of their food choices do so—the phenological advancement effect gets diluted in the overall diet. In another example, Betzholtz & Franzen (2011) found that, while monophagous species are usually associated with less mobility, lower capacity to adapt, and higher risk of decline in abundance, such species may display higher levels of mobility when their larval food plant is rare and unevenly distributed. In those cases, species may have adapted to move more in search of their food plant, and as a consequence can be able to move over a wide geographic area. Another study highlighting unexpected responses to warming (Pateman et al. 2012) found that the brown argus butterfly *Aricia agestes* (Lepidoptera: Lycaenidae) shifted its larval food plant *Helianthemum nummularium* (Cistaceae) to the more readily and widely available *Geranium molle* (Geraniaceae), and consequently has expanded its range northwards at a faster pace than would be expected.

Species-specific responses to climate change can also lead to whole different environmental outcomes as a consequence of the lepidopteran response. For instance, Altermatt (2010) suggests that species with herbaceous plants in their diets will respond by advancing their activity or having a second generation, leading to higher defoliation of herbaceous plants, and therefore climate change-related phenology shifts in herbivore communities may be different for woodlands compared to grasslands or herbaceous agricultural systems. Herbaceous-rich grasslands might see an increase in herbivory by Lepidoptera, while forested areas might not. However, climate change may also lead to changes in growth of a food plant, which can change the nature of the herbivore-plant interaction (Hamilton et al. 2012), or alter the chemical contents of plants, affecting the species that interact with it (Casteel et al. 2012)

Some late-flying species at high elevations may have their flight period synchronized with each other, and not respond to climate change in the predicted ways. A study by Gutierrez Illán et al. (2012) found that the flight phenology of butterfly species with such characteristics on a Mediterranean mountain range did not have a significant elevational delay as expected. They argue that local adaptations to ensure timing of resources or other condition might be occurring in such species, and therefore the conservation planning for some species in mountain landscapes might require more data spanning a wide range of habitat or topographic conditions, so that a true depiction of the species phenological responses can be assessed.

CONCLUSION

Lepidoptera conservation under a changing climate needs to be addressed in a comprehensive manner, taking into account as many relevant interactions as possible, considering all possible threats and testing among the alternatives. As stated by Pau et al. (2011), accurately forecasting phenology is a desirable objective, but there are different perspectives and approaches offered in the literature.

The use of phenology data for resource management and conservation planning is relevant when one knows the implications of the observed phenological changes, as well as what to do about those changes. Lepidoptera flight phenology can have wide implications ranging from habitat integrity, species conservation, and essential interactions, to the management of agricultural pests and invasive species. A species that advances its flight period will likely reproduce earlier, and its impacts on resources can be significant. The timing of conservation and management practices such as timed burns, crop sowing, or pest monitoring and management may have to be adjusted in order to maintain the basic processes of a landscape, agricultural operation, or other area of interest. In addition, a longer growing season accompanying warmer temperatures may also mean a second generation of an agricultural pest that advances its flight period, or a disruption in the effect of its natural enemies, which may not respond to temperatures synchronously.

Changes in phenology can ultimately translate into changes in abundance or performance for many species, and the knowledge of possible outcomes may provide early warning of such events, and inform further conservation or management measures to protect the organism, habitat, or other unit of interest. Understanding the impacts that can be relevant to management and planning for the appropriate responses that will effectively deal with phenological changes will be an essential component of conservation planning under a changing climate.

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