

**IJEE SOAPBOX:
CHARISMATIC MESOFAUNA: BUTTERFLIES AS
INSPIRATION AND TEST FOR THEORY THAT
INTEGRATES ECOLOGY AND EVOLUTION**



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A person must have a heart of stone to glimpse a butterfly flickering in flight across a sun-dappled field, and not feel a little frisson of simple joy at the sight. The editors of this useful and timely compendium in their introductory remarks (Pe'er and Settele, 2008a, this issue) aptly observe that much of the public's sympathy for butterfly conservation comes from the "beauty and charisma of butterflies". The papers collected here highlight many important issues in the conservation of butterfly populations, from fundamental biological issues such as characterizing movement across landscapes (Hovestadt and Nowicki, 2008, this issue) and gauging climate drivers of community structure (Schwartz-Tzachor et al., 2008, this issue), to the use of butterflies as bioindicators (Pe'er and Settele, 2008b, this issue), to very practical issues emerging from engagement of the public in conservation efforts (Kühn et al., 2008, this issue). Schultz and Crone (2008, this issue) have carried out an intriguing survey of academics and practitioners concerned with butterfly ecology in order to assess which areas of ecological theory have been most useful in practice. The overwhelming response was metapopulation biology, which in essence emphasizes the role of space and disturbance in driving population dynamics. The editors in their introduction (Pe'er and Settele, 2008a, this issue) amplify this theme, suggesting that a primary challenge facing our field is to integrate ecological processes across spatial scales from the level of individual movement decisions to that of macroecological and biogeographical patterns. I concur with this suggestion. In my brief remarks here, I will reflect on an important problem at the interface of ecology and evolution where in my opinion there could be a much more fruitful interplay of theory and empiricism, a problem where the study of butterflies may be "pre-adapted" to play an exemplary role.

The problem also often involves space, and is related to conservation, but in different ways than emphasized in the papers in this issue. Like all organisms, butterflies

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have limited distributional ranges, and often these ranges are correlated with climatic variables. Studies of shifts in butterfly range limits, both latitudinally and altitudinally, have been at the forefront of documentation of the biological impact of global climate change, with, for instance, many northward expansions and southern retractions of butterfly ranges across Europe (Parmesan et al., 1999), and contractions up mountain slopes associated with shrinking snowpacks (e.g., *Euphydryas editha*; Parmesan, 1996) and warming temperatures (sixteen montane butterfly species in Spain; Wilson et al., 2005).

At the receding edge of a species range, local populations in a certain sense are pulled by directional environmental change into circumstances “outside the niche”. This raises the general question: when can evolution occur sufficiently fast to rescue a species placed outside its niche and facing extinction (Pease et al., 1989; Holt, 1990; Gomulkiewicz and Holt, 1995)? This is part of the broad problem of understanding both niche conservatism—which is the observation that species may seem to have much the same niche limits over a broad geographical range, or over long swaths of evolutionary history (Bradshaw, 1991; Holt and Gaines, 1992; Wiens and Graham, 2005)—and rapid niche evolution (Reznick and Ghalambor, 2001).

Butterflies can evolve quite rapidly in ways that could influence their distributional limits. For instance, Singer et al. (1993) demonstrated that the checkerspot *Euphydryas editha* shifted in its preference from a traditional host, *Collinsia parviflora*, to a novel host, *Plantago lanceolata*, over just eight years, and that this difference reflected genetic change. If the two host species have different geographical distributions, this shift in host use could then precipitate a large shift in the butterfly’s range. Dispersal traits can likewise evolve rapidly. Hill et al. (1999) report that as the speckled wood butterfly (*Pararge aegeria*) in the United Kingdom spread north, individuals in the new populations had both larger thoraxes and a greater ability to fly, suggesting rapid evolution in dispersal traits. Geographical ranges reflect both niches and dispersal, and evolution in either could lead to evolved shifts in the range.

But in other cases, butterfly niches can be conserved, even over very large distances across a range. A very interesting example of what looks like niche conservatism has been reported for the Sachem skipper *Atalopedes campestris* by Crozier and Dwyer (2006). These authors developed a suite of detailed models relating specific demographic parameters to temperature, across the annual cycle. These submodels were generated from careful field studies in the state of Washington, and then combined into an overall population model, which predicted λ (annual population growth rate) as a joint function of summer and winter temperature. The model helps explain recent shifts in the northern edge of the species’ range (Crozier, 2003, 2004). Figure 2 in Crozier and Dwyer (2006) depicts the current distribution of the butterfly across North America, along with the model predictions. The model does very well in the Pacific Northwest, where the field data were collected. What to my eye is remarkable is that the model does equally well in the northeastern United States. It does less well in the interior (where strong winds lead to establishment of ephemeral populations), but in the two regions at opposite ends of the continent with more stable maritime climates, the niche limit that has been quan-

tified and understood demographically at the northern limit of the species in the state of Washington, also does quite well in explaining the northern limit of the species in southern New England. Thus, one basic aspect of the niche of this species—the thermal environments in which it can persist, versus where it declines toward extinction—appears to have been conserved over an enormous distance.

Understanding what accounts for niche conservatism, and predicting when one should instead expect rapid niche evolution, is a vitally important problem, both in basic ecology and biogeography, and in the applied sciences. Many problems in conservation biology, invasive species, and emerging diseases at base involve the issue of evolution of species' niches. Much of the literature on niche conservatism to date is essentially phenomenological in nature, reporting correlations between species distributions and various environmental attributes (“ecological niche models”). There is nothing at all wrong with this, and it indeed provides an essential starting point, but what in my opinion is really needed at this juncture is a deeper mechanistic understanding of the factors that either constrain or facilitate niche evolution. This understanding requires one to take a highly integrative approach to science, as explanations for niche conservatism can reflect a wide spectrum of forces and constraints, from limitations on genetic variation (Bradshaw, 1991), to tradeoffs emerging from how organisms are engineered from the gene to the whole phenotype (Hansen and Houle, 2004), to the details of demography and spatial movement patterns (Holt and Gaines, 1992; Kawecki, 1995; Holt, 1996), to the nexus of interspecific interactions (Ackerly, 2003; Case et al., 2005).

I do not myself work with butterflies, but they seem to me to have many of the traits one would want for systems where this question is being seriously addressed. A great deal is known about the basic biology of many butterfly species (e.g., Ehrlich and Hanski, 2004). They can often be raised in the lab, permitting detailed genetic and functional studies of key traits. They have short generations, which means there is a reasonable hope of seeing evolutionary change within a human generation. They are popular and diurnal, so, like birds, much is known about their basic natural history and geographical distributions. They are ectotherms, hence sensitive to thermal conditions, and their dependence upon host plants as larvae means one can readily quantify resource dimensions for this essential life history stage. They often are involved in strong interactions with other species (host plants, predators, parasitoids; e.g., van Nouhuys and Hanski, 2005; Anton et al., 2007; Pe'er and Settele, 2008b, this issue), which makes the interspecific dimensions of the niche amenable to quantitative modeling (e.g., Mouquet et al., 2005).

I suggest that these traits collectively make butterflies potentially highly useful in developing a deeper understanding of the phenomenon of niche conservatism. This would be a satisfying intellectual endeavor in its own right. Beyond that, to return to the theme of this special issue, grappling with the issue of niche conservatism may provide insights useful in the conservation of endangered species. Conservation problems arise in the first place because the world changes in ways that species are restricted in their abundance and distribution, and in the most severe cases because species are pushed outside their ecological niches. And in the second place, conservation problems arise because

species so pushed do not evolve by natural selection to persist in novel environments. So conservation problems reflect a seeming “failure” of evolution by natural selection to adapt to novel environments, a kind of failure we dub “niche conservatism” (Holt and Gomulkiewicz, 2004). My hope is that we might sometimes be able to mollify environmental change so as to facilitate, rather than unwittingly hamper, the power of adaptation by natural selection, to at times permit the evolutionary rescue of species trying to cope with change. Given the pace of environmental change we are inflicting upon the rest of the diversity on the planet, Lord knows the living world needs all the help it can get.

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