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Review

More than just indicators: A review of tropical butterfly ecology and conservation

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Abstract

Roughly 90% of butterfly species live in the tropics. Despite this, we know very little about tropical butterfly ecology particularly when compared to temperate butterfly systems. The relative scarcity of data on tropical butterfly populations hampers our ability to effectively conserve them. In this review we summarize recurring themes from ecological research on tropical butterflies to serve as a framework for understanding their conservation. Key themes include: (1) the tropics represent the evolutionary origins of butterfly diversity, (2) while some tropical butterflies exhibit relatively stable population dynamics, longer-lived adult stages, and more continuous age-specific reproduction compared to temperate zone species, the generality of these patterns is debatable, and (3) complex species interactions (e.g. mimicry, parasitism and predation) can have significantly greater influences on ecological and evolutionary processes in tropical butterflies than in temperate ones. This state of ecological knowledge, combined with scarce resources, has traditionally constrained tropical butterfly conservation efforts to habitat level approaches, unlike the species- and population-specific approaches familiar in North America and Europe. Consequently, much conservation research on butterflies in the tropics has focused on the

relationship between habitat quality (e.g. forest fragmentation) and butterfly diversity, though predictive patterns even in this regard remain elusive. We argue that with the increasing threats of habitat destruction, fragmentation and climate change, it is necessary to move beyond this diversity and habitat relationship if we are to improve predictive capabilities when evaluating anthropogenic impacts on tropical butterfly communities. Tropical butterflies are more than just useful indicator species. They represent some of the most spectacular and visually appealing organisms in the world and play many vital roles in tropical ecosystems. We hope that this synthesis will lay the groundwork for future ecological studies of tropical butterfly populations, species, communities and conservation.

Introduction

The biodiversity crisis is expected to severely impact insect species (Pimm and Raven, 2000). Yet, of the approximately 40000 insect species already estimated to have gone extinct over the past 600years, only 70 have been documented, half of which were Lepidoptera (Dunn, 2005). The likely more serious issue of insect *population* extinctions is even less well known. Considering that less than one million insect species have been described out of 5–10 million believed to exist (Gaston, 1991), all of these observations indicate that many insect species likely to go extinct as a result of human impacts have not even yet been named or described (Samways, 2007) and that these insect populations are disappearing daily in large numbers, unheralded.

If we are to have any chance of effectively conserving insect populations globally, we must understand their ecologies. This puts a spotlight on butterflies, because of all insects, butterflies are probably the best known taxonomically and ecologically (Thomas, 2005). Indeed, the study of butterfly biology has a long history and has contributed greatly to our understanding generally of ecology, evolution, biogeography and conservation (Bates, 1862, Müller, 1879, Wallace, 1865, Wallace, 1879, Fisher et al., 1943, Gilbert and Singer, 1975, Boggs et al., 2003, Mallet, 2004).

However, our knowledge of tropical butterflies is deficient when compared to their temperate counterparts. Consider the following rough, but telling, exercise. We conducted a BIOSIS search for papers from 1990 to 2000 for “Lepidoptera” and “England” and found there were 1287 papers. That same search for “Lepidoptera” and “Brazil” however only results in 679 papers. Brazil is over 30 times as large as England, has over 50 times as many butterfly species (58 species in England cf. Pollard and Yates, 1993 vs. 3300 in Brazil cf. Brown, 1996), but has half the studies of England. When you also consider that Brazil is comparatively one of the best studied tropical regions in the world (Stocks et al., 2008;

though to be fair England is one of the best-studied temperate countries), you can get a feel for the problem.

The difference in butterfly knowledge between tropical and temperate regions has consequences for their conservation. While US and UK butterfly conservation efforts are mainly species-specific, in the tropics knowledge and resource limitations dictate "habitat protection" approaches with little regard to inclusion of information or tools from butterfly population-level or species-specific conservation (New et al., 1995, New, 2009). Consequently, appropriations of recent advances in ecological theory have been slow for tropical conservation. For example, in a survey of 27 butterfly biologists, over 80% named "metapopulation theory" as an important concept guiding butterfly conservation; tellingly, none of the examples they gave to illustrate the utility of metapopulation or any other ecological theories were tropical (Schultz and Crone, 2008).

The habitat level conservation approach for butterflies practiced throughout much of the tropics has lead to a proliferation of studies examining butterflies' indicator potential for assessing processes such as habitat degradation and land use (e.g. Daily and Ehrlich, 1995, Hill, 1995, Brown and Freitas, 2000, Bobo et al., 2006, Akite, 2008, Bonebrake and Sorto, 2009, Uehara-Prado and Freitas, 2009). Fleishman and Murphy (2009), among many others (e.g. Kremen, 1992, Lawton et al., 1998), suggest that only under limited circumstances may butterfly species be reliable indicators of environmental change and that the widespread usage of the indicator concept in butterflies can be and has been problematic. However, the use or misuse of butterflies as indicators of environmental change in the tropics is not our main concern here. Instead, we argue that even if butterflies *are* good indicators they are also much more than that. They play a diversity of ecological roles, interest lay people in biology and conservation in general and insects in particular, and should be valued beyond their utility as indicators.

To that end, we review the literature on tropical butterfly ecology and conservation in hopes that we might advance beyond "habitat protection" as essentially the sole conservation tool in the tropics. We summarize research on tropical butterfly biogeography, life history, demography and species interactions to highlight the differences and similarities between temperate and tropical butterfly ecology. Then, we look at the threats to diversity in the tropics and end with directions for future research and recommendations on how to improve our ability to conserve tropical butterflies, and through them tropical biodiversity. Taxonomically we focus on "true butterflies" (Papilionoidea) but recognize the role of all Lepidoptera, including in particular large moths (e.g. Bombycoidea) and skippers (Hesperioidae), to conservation and ecology. Geographically we focus on the tropics, or

butterfly populations that reside between the tropics of Capricorn and Cancer, but also discuss temperate butterfly biology for comparative uses.

Section snippets

Global distribution and evolutionary origins

The world contains roughly 18000–20000 species of butterflies and there is a clear latitudinal gradient in butterfly species diversity, with numbers highest in the tropics (Shields, 1989, Larsen, 2005). How many butterfly species are tropical? It is difficult to give a precise estimate given the continual updating of checklists and splitting and lumping of species worldwide, the difficulties of defining "tropical," and the "tropical" species that extend into largely temperate zones and the…

Demography and life history

While the population biology of butterflies has been well studied in some systems, there has been a comparative dearth of tropical butterfly population biology studies (Ehrlich, 1984). Studying *Heliconius ethilla*, Ehrlich and Gilbert (1973) conducted the first explicitly comparative long-term study between a tropical butterfly population and temperate populations. The relatively constant population size, delayed reproduction, and high adult survivorship of the *H. ethilla* population led Ehrlich…

Species interactions

The complex array of species interactions, or the "biotic environment", may be the most defining characteristic of tropical environments (Dobzhansky, 1950). In particular, the close relationship between butterflies and their host plants has been a recent focus as one explanation for tropical "megadiversity", though patterns globally remain unclear (see for discussion and examples: Stork, 2007, Lewinsohn and Roslin, 2008). Beyond larval host plant and adult resource interactions, predatory,…

Monitoring

As defined by Yoccoz et al. (2001), monitoring efforts seek to gather information "at different points in time for the purpose of assessing system state and drawing inferences about changes in state over time". The goals and objectives of specific monitoring programs

are critical in devising monitoring methodology. That is “unfocused” or “omnibus” surveillance monitoring can be an inefficient use of conservation resources (New, 2006, Nichols and Williams, 2006). Extensive and exemplary…

Habitat loss

Habitat loss in the tropics can take many forms including conversion to agriculture, logging or fragmentation. For Lepidoptera, conversion to agriculture might be the most destructive form of habitat loss (Dunn, 2004, Sodhi et al., 2009). However, making definitive claims about habitat disturbance effects on butterfly species diversity is difficult given the variety of responses butterflies exhibit to disturbance (Koh, 2007; Table 1). Koh (2007) reviewed 20 studies that examined the impacts of…

Future research

Studies of butterflies as indicators of disturbance and environmental change have been useful for conservation efforts that focus on reserve design (Kremen, 2003) and landscape connectivity or corridor establishment (Hill, 1995, Brown and Freitas, 2000). However, the difficulty in reaching generalizations about the effects of anthropogenic development or habitat loss on butterfly diversity (e.g. Koh et al., 2004) stems from a poor understanding of basic tropical butterfly ecology. If we are to…

Acknowledgments

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> ...Despite their apparent importance, insects are often neglected in studies on ecosystem function and conservation assessments (Chowdhury et al., 2022a; Di Marco et al., 2017; Dunn, 2005; Geyle et al., 2021; Samways, 2007; Taylor et al., 2018); however, butterflies, to some extent, are an exception because the taxonomy, geographic distribution and status of many species are relatively well known (Schultz et al., 2019; Schulze et al., 2004). Butterflies are good indicators of habitat quality as well as general environmental health (Bonebrake et al., 2010; Dennis et al., 2003; Kunte et al., 2012), are sensitive to disturbance and changes in their habitat, and can severely be affected by environmental changes, including abiotic factors - such as temperature, light intensity, soil composition, radiation, humidity, photoperiod, and changes in the forest structure (Aich et al., 2016; Whitworth et al., 2018; Shahriar et al., 2020). Even minor changes in their habitat can lead to either migration or local extinction (Bonebrake et al., 2014; Chowdhury et al., 2017; Thomas et al., 2006; Chowdhury et al., 2021c,d)....

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