Synopsis and the Future of Caterpillar Research



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The most extraordinary instance of imitation I ever met with was that of a very large caterpillar, which...startled me by its resemblance to a small snake. The first three segments behind the head were dilatable at the will of the insect, and had on each side a large black pupillated spot, which resembled the eye of the reptile: it a poisonous or viperine species mimicked, and not an innocuous or colubrine snake, this was proved by the imitation of keeled scales on the crown, which was produced by the recumbent feet, as the caterpillar threw itself backwards. (HW Bates 1863, The Naturalist on the River Amazons, p. 509)

Caterpillar Biology and Ecology in a Tritrophic World

Beginnings Along the Amazon

Henry Bates was one of the early naturalists who first documented the unusual appearance and behavior of caterpillars, as well as interactions between caterpillars, their host plants, and their natural enemies. This early research was foundational to all that appears in this volume. It involved observations of adult oviposition, host plant associations, the behavior of caterpillars on their host plants and with their natural enemies, rearing caterpillars to adulthood, recording changes in morphology and behavior from one instar to the next, and discovering the environmental conditions necessary for successful pupation and eclosion to adulthood.

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As a result of Bates' work, a number of major ideas in ecology and evolution were first born. These include tritrophic interaction theory (Hairston et al. 1960; Price et al. 1980; Abdala-Roberts et al. 2019), coevolution between plants and angiosperms (Brues 1924; Ehrlich and Raven 1964), mimicry theory (Bates 1862), chemical ecology (e.g., Brower et al. 1968; Reichstein et al. 1968), and some of the first evidence for adaptations as the outcome of natural selection (Darwin 1862).

Advances in Technology

In the absence of analog or digital photography, early caterpillar biologists documented their subjects by drawing and/or painting them on paper. We have come a long way since then: technology is making the study of caterpillars and their role in an anthropocentric world much more feasible. Since Stamp and Casey's (1993) landmark volume, numerous advances allow us to understand more completely the biology of caterpillars. To start, we now have the ability to identify caterpillars to species level, using DNA barcoding, without resorting to rearing to adulthood. This technology can be an enormous time-saving, particularly for projects studying the community ecology of caterpillars in temperate regions where faunas are more well known. It is also most convenient when the exact conditions have not been discovered that result in successful pupation and eclosion. Still, nothing can take the place of identification based on updated taxonomy. Family and subfamily taxonomic treatments at the global level (e.g., Marquis et al. 2019b) are sorely needed at this time.

We can sequence caterpillar genes and modify those genes in traditional model organisms (Drosophila melanogaster), to assemble the evolutionary history of adaptations allowing caterpillars to feed on toxic host plants (Karageorgi et al. 2019; Groen and Whiteman, Chapter "Ecology and Evolution of Secondary Compound Detoxification Systems in Caterpillars", this volume). Gene sequencing and directed biochemistry allow us to understand how plant material is metabolized once ingested. The network analysis of plants, their herbivores, and associated natural enemies, not widely available as tool to ecologists in 1993, when the Stamp and Casey volume was published (Ings and Hawes 2018), allows us to picture the role of caterpillars in ecosystems (Salcido et al., Chapter "Plant-Caterpillar-Parasitoid Natural History Studies Over Decades and Across Large Geographic Gradients Provide Insight into Specialization, Interaction Diversity, and Global Change", this volume). The techniques and associated data analysis methods are now available to quantify the metabolome of entire host plants with the goal of discovering just which plant traits influence host plant use by caterpillars (e.g., Endara et al., Chapter "Impacts of Plant Defenses on Host Choice by Lepidoptera in Neotropical Rainforests", this volume). Even more recent than network analysis of species, the development of network analysis of secondary metabolites promises to reveal the evolutionary history of secondary metabolite pathways (Sedio 2017). This should bring us one step closer to understanding the coevolutionary history between vascular plants and Lepidoptera.

We now have the tools to characterize the microbiome, the rich assemblage of microorganisms found within and on the surface of caterpillars, and how they influence the ability of the insect to successfully complete development (Hammer and Bowers 2015; Hammer et al. 2017). Finally, many of the questions that caterpillar biologists are puzzled by require large teams of researchers at multiple, protected locations to collect sufficiently large data sets to answer those questions. These teams have been assembling over the years and are making rapid advances. Large data sets are being gathered, requiring advances in statistical analysis (Braga and Diniz, Chapter "Trophic Interactions of Caterpillars in the Seasonal Environment of the Brazilian Cerrado and Their Importance in the Face of Climate Change", this volume; Boege et al., Chapter "Impacts of Climatic Variability and Hurricanes on Caterpillar Diet Breadth and Plant-Herbivore Interaction Networks", this volume; Salcido et al., Chapter "Plant-Caterpillar-Parasitoid Natural History Studies Over Decades and Across Large Geographic Gradients Provide Insight into Specialization, Interaction Diversity, and Global Change", this volume). Citizen science is just coming into its own, allowing geographically widespread collection of original data and observations (e.g., iNaturalist: Pierce and Dankowicz, Chapter "The Natural History of Caterpillar-Ant Associations", this volume) and making important contributions in the area of bird and insect conservation. Certainly, the research outlined in Chapter "Caterpillar Patterns in Space and Time: Insights From and Contrasts Between Two Citizen Science Datasets" (Di Cecco and Hurlbert) and Chapter "Plant-Caterpillar-Parasitoid Natural History Studies Over Decades and Across Large Geographic Gradients Provide Insight into Specialization, Interaction Diversity, and Global Change" (Salicido et al.) reveals the major contributions that the general public can make to caterpillar science. At a smaller scale, but no less important, many important questions require teams of geneticists, organic chemists, biochemists, microbiologists, and neurobiologists to answer questions that intrigue the caterpillar biologist (Groen and Whiteman, Chapter "Ecology and Evolution of Secondary Compound Detoxification Systems in Caterpillars", this volume).

Forces Driving Coevolution

Major advances in ecology and evolution are represented on the pages of this book, with a focus on how caterpillars relate to neighboring trophic levels. A tritrophic view of the caterpillar world is one that drives much of current research in caterpillar ecology. Caterpillars are "sandwiched" between their neighboring trophic levels (Abdala and Mooney 2015). There is mounting evidence that their biology thus represents a compromise between dealing with nasty food plants and nasty natural enemies (Lill and Weiss, Chapter "Host Plants as Mediators of Caterpillar-Natural Enemy Interactions", this volume). The pages of this book are replete with examples of these trade-offs.

Contrary to the more traditional view of reciprocal adaptation between plants and insects (Ehrlich and Raven 1964), caterpillars and other herbivorous insects may readily switch host plants over evolutionary time, at least ones that share similar defensive profiles (Endara et al., Chapter "Impacts of Plant Defenses on Host Choice by Lepidoptera in Neotropical Rainforests", this volume). In the Inga system (Fabaceous tropical tree), while herbivores collectively select for rapid divergence in host defenses, the lack of congruence between phylogenies of hosts and herbivores supports frequent host shifts (see also Dobler et al. 2012). These results call into question how often reciprocal coevolution comes into play between plants and their insect herbivores. In contrast, results from the Inga system suggest that insects are jumping to new hosts repeatedly, imposing little diversifying selection on their hosts. Shaking the foundation even more, Singer et al. (Chapter "Predators and Caterpillar Diet Breadth: Appraising the Enemy-Free Space Hypothesis", this volume) present evidence that predators must be considered as possible instigators of host plant shifts (see also Murphy 2004). Thus, secondary plant chemistry may no longer be the single linchpin upon which co-diversification depends. Importantly, it is likely that there is some combinatorial effect of the first and third trophic levels that influence host plant shifts (Lill and Weiss, Chapter "Host Plants as Mediators of Caterpillar-Natural Enemy Interactions", this volume).

Defenses Against Natural Enemies

A traditional view of caterpillars as prey is that they employ one of two general strategies to escape their natural enemies. One strategy is to forgo chemical and physical defense, escaping natural enemies by visual camouflage, either by crypsis (background matching) or by masquerade, resembling an inedible object (Skelhorn et al. 2010; Higginson et al. 2012; see examples in Wagner and Hoyt, Chapter "On Being a Caterpillar: Structure, Function, Ecology, and Behavior", this volume). Alternatively, they may sequester or manufacture defensive compounds de novo to make themselves distasteful, often accompanied by aposematic coloration. Bowers (Chapter "Sequestered Caterpillar Chemical Defenses: From "Disgusting Morsels" to Model Systems", this volume) has spent a career studying this latter strategy, building on the early theoretical writings of Darwin, Bates, and Wallace, and on experiments by Rothschild and the Browers, to understand the details of the phenomenon: how do host plant chemistry and caterpillar species identity together affect sequestration level, how much is sequestered, and how do host plant age and caterpillar instar affect the process? Despite the fact that sequestration occurs throughout the Lepidoptera phylogeny (and in many other insect orders), Bowers' chapter reveals that we know much less about the actual adaptive advantages of chemical sequestration in terms of escape from natural enemies.

In some cases, sequestration may actually reduce the immunocompetence of caterpillars against parasitoids (Ode, Chapter "Caterpillars, Plant Chemistry, and Parasitoids in Natural vs. Agroecosystems", this volume; Smilanich and Muchoney, Chapter "Host Plant Effects on the Caterpillar Immune Response", this volume). This begs the question as to the adaptive targets of sequestration, whether the enemies are vertebrates, predatory arthropods, parasitoids, or some combination thereof. Singer et al.'s analysis (Chapter "Predators and Caterpillar Diet Breadth: Appraising the Enemy-Free Space Hypothesis", this volume) suggests that sequestration is most effective against vertebrate predators. This question is not only important to ecologists and caterpillar biologists, but is immensely important in agriculture. We rely upon natural enemies, either introduced or native, to provide at least partial control of caterpillar pests in crop systems (Garfinkel et al. 2020). At the same time, we select for plant phenotypes that are sometimes elevated and sometimes diminished in secondary compounds. What is the corresponding effect of altered host chemistry on caterpillar phenotypes, and in turn, the vulnerability of the caterpillars to their natural enemies? Is vulnerability reduced compared to less managed ecosystems? Detailed studies of these interactions in agricultural systems are limited to a relatively few crop species, perhaps no more than 15 in total (Ode, Chapter "Caterpillars, Plant Chemistry, and Parasitoids in Natural vs. Agroecosystems", this volume).

Kauer et al. (Chapter "Surface Warfare: Plant Structural Defenses Challenge Caterpillar Feeding", this volume), Groen and Whiteman (Chapter "Ecology and Evolution of Secondary Compound Detoxification Systems in Caterpillars", this volume), Pierce and Dankowicz (Chapter "The Natural History of Caterpillar-Ant Associations", this volume), and Koptur et al. (Chapter "Caterpillar Responses to Ant Protectors of Plants", this volume) suggest a third adaptive option for caterpillar lineages in the face of natural enemy attack: chemicals may be synthesized or sequestered and used not as deterrents but as camouflage such that natural enemies do not recognize the larvae as prey. We do not know whether chemistry itself can provide sufficient camouflage or whether chemistry, morphology, color, and behavior may work in concert to provide protection from enemies. This hypothesis has been the subject of little study outside of caterpillar interactions with ants, where chemistry is known to be important in the evolution of caterpillars that co-op ant behavior for their own protection. Here ants, normally predators, become protectors, providing caterpillars with enemy-free space (Pierce and Dankowicz, Chapter "The Natural History of Caterpillar-Ant Associations", this volume). Although most diverse and widespread in the Riodinidae and Lycaenidae, caterpillar-ant symbioses have evolved at least 25 times in disparate lines scattered across the Lepidoptera phylogeny.

There is yet another strategy evolved by caterpillars to provide protection against natural enemies, and in some cases to mitigate low host plant quality and ameliorate a stressful abiotic environment, all simultaneously. Numerous clades of caterpillars have evolved the ability to use plant parts plus silk, and sometimes frass, to build "shelters" on their host plant (e.g., Braga and Diniz, Chapter "Trophic Interactions of Caterpillars in the Seasonal Environment of the Brazilian Cerrado and Their Importance in the Face of Climate Change", this volume). These shelters can provide protection against predators (e.g., Baer and Marquis 2020, 2021), but they may increase susceptibility to attack by parasitoids (e.g., Gentry and Dyer 2002).

The factors that determine the balance between reduced versus increased susceptibility depending on the natural enemy type are not known. The presence of these caterpillar-built shelters can have important implications for arthropod community structure on their host plants. The shelters are often subsequently occupied by other arthropods, often resulting in novel communities of host-associated arthropods not seen on shelter-free host plants. Marquis et al. (Chapter "The Impact of Construct Building by Caterpillars on Arthropod Colonists in a World of Climate Change", this volume) present a predictive model of the impacts of such "shelters" on community structure, depending on the structure of the shelter and the behavior of the caterpillar shelter-builder. Shelter-building caterpillars comprise a large portion of the diversity of Lepidoptera, but their effects on other arthropods through sharing of host plants have been studied only recently.

Development of Caterpillars in a Tritrophic World

A true frontier for future caterpillar research is the study of how developmental stage (instar) influences the myriad interactions between the caterpillar and its adjoining trophic levels. Each chapter of this book touches on this topic either directly or indirectly. Most current ecological data come from the study of late instars, as they are the easiest to work with. Early instars are often overlooked in ecological sampling, difficult to identify when found, and just as easily lost when collected. And yet profound effects are revealed when instar is incorporated into experimental and sampling designs.

Caterpillars frequently vary dramatically from one instar to the next not only in size but in color, shape, setal covering, and internal morphology. Often, changes are so dramatic that the uninitiated could understandably classify early and late instars as different species (Plates 1 and 2). Lepidopteran larvae show more diversity of form among instars and among species than all other herbivorous orders. It is this diversity of form that draws us to them. Part of this diversity must arise from the fact that hemimetaboly constrains development in other phytophagous orders: the Orthoptera, Phasmatodea, and Hemiptera. The Coleoptera, which are holometabolous, are speciose, but their larvae are generally not as diverse in form as those of Lepidoptera, and they show relatively less change with ontogeny. Most herbivorous species of Coleoptera are internal plant feeders. These observations lead to the reasonable hypothesis, yet to be tested, that interactions between host plants, caterpillars, and the third trophic level have given rise to much of the diversity of form and function seen in caterpillars, both during development and across species (see also Wagner and Hoyt, Chapter "On Being a Caterpillar: Structure, Function, Ecology, and Behavior", this volume). It also suggests that the greatest diversity in form will be found in externally feeding caterpillars.

These changes in external and internal caterpillar morphology influence how the caterpillar interacts with its host plants, natural enemies, and other non-predator arthropods. Caterpillars change in behavior with instar (e.g., parts of leaf consumed,

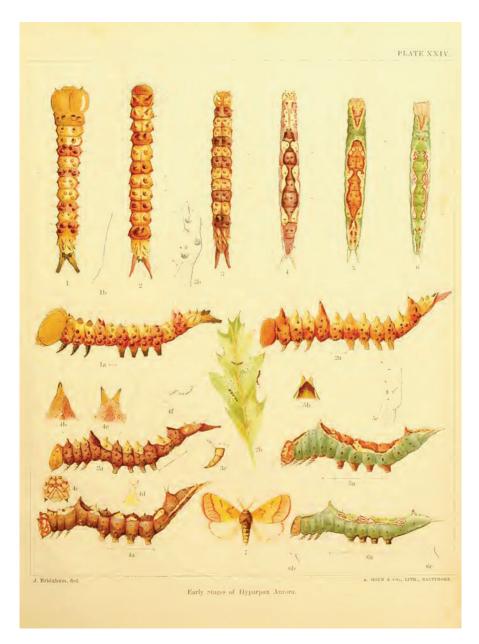


Plate 1 Variation in size, color, and morphology from one instar to the next in *Hyparpax aurora* (Smith) (Notodontidae) (Plate XXIV of Packard (1895))

Fig. 1 Stage I (first instar), dorsal view; (1a) side view; (1b) dorsal piliferons tubercule

Fig. 2 End of Stage I; (2a) side view; (2b) freshly hatched larvae, natural size

Fig. 3 Stage II (second instar); (3a) side view; (3b) third abdominal segment, side view; (3c) a thoracic leg

Fig. 4 Stage III (third instar); (4a) side view; (4b) dorsal tubercle; (4c) front view of the same; (4d) subdorsal tubercle; (4e) face; (4f) natural size

Fig. 5 Stage IV (fourth instar); (5a) side view; (5b) dorsal tubercle of the eighth abdominal segment; (5c) third abdominal segment, side view

Fig. 6 Last stage (fifth instar); (6a) side view; (6b) dorsal tubercle of the first abdominal and (6c) eighth abdominal segment

Fig. 7 Adult male, natural size

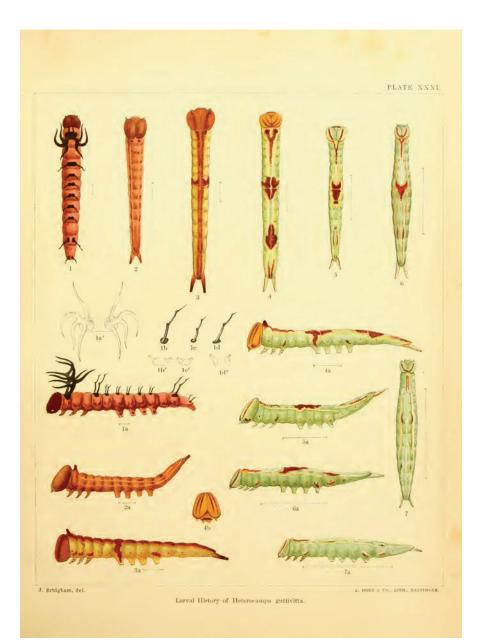


Plate 2 Variation in size, color, and morphology with instar in *Heterocampa guttivitta* (Smith) (now *Cecrita guttivitta* Walker) (Notodontidae) (Plate XXXI of Packard (1895))

Fig. 1 Stage I (first instar); (1a) side view; (1a') prothoracic antlers; (1b, 1b') antlers on the first abdominal segment; (1c, 1c') antlers on the second to the seventh abdominal segments; (1d, 1d') antlers on the eighth abdominal segment

Fig. 2 Stage II (second instar); (2a) side view

- Fig. 3 End of Stage II; (3a) side view
- Fig. 4 (4a) Stage III (third instar)
- Fig. 5 (5a) Stage IV (fourth instar)
- Fig. 6 (6a) End of Stage IV
- Fig. 7 (7a) Stage V (fifth instar)

level of aggregation, ballooning, internal vs. external feeding, shelter structure) (Zalucki et al. 2002). Food quality experienced by early instars can influence the subsequent phenotype of later instars, even so far as affecting caterpillar coloring and morphology (Akino et al. 2004; Koptur et al. 2015) and larval diapause (Hunter and McNeil 1997).

The tritrophic world in which caterpillars exist looks profoundly differently from the view of a 1-mm-long first instar than that of an 8-cm-long (or longer) fifth instar caterpillar (e.g., Packard 1895). To early instar caterpillars, leaf hairs can be an impenetrable, dangerous chaparral, in some cases full of barbs that can puncture the cuticle (Gilbert 1971), preventing access to the actual leaf surface (Zalucki et al. 2002). Even on glabrous leaves, the surface texture takes on a vastly different landscape for the early versus late instar caterpillar (Kauer et al., Chapter "Surface Warfare: Plant Structural Defenses Challenge Caterpillar Feeding", this volume). We see, as a result, different strategies for dealing with plant morphological defenses as caterpillars mature (e.g., Keathley and Potter 2011; Kariyat et al. 2018; Boege et al. 2019; Kauer et al., Chapter "Surface Warfare: Plant Structural Defenses Challenge Caterpillar Feeding", this volume).

The landscape of natural enemies and abiotic threats also changes with instar (Boege et al. 2019). Early instar caterpillars may be too small to be vulnerable to bird predation, but they are susceptible to predation by arthropods (Singer et al. 2017). As they mature, they are subject to a shifting community of parasitoids from early to late instars (Stireman and Shaw, Chapter "Natural History, Ecology, and Human Impacts on Caterpillar Parasitoids", this volume). Instar affects the likelihood of predation by ants, as demonstrated frequently for caterpillars found on plants with extrafloral nectaries (Koptur et al., Chapter "Caterpillar Responses to Ant Protectors of Plants", this volume and references therein). Instar also affects sequestration (Quintero and Bowers 2018; Jones et al. 2019), de novo chemical synthesis (Frankfater et al. 2009), susceptibility to predation by non-ant predators (e.g., Schwenk et al. 2010; Singer et al. 2017; Baer and Marquis 2020), and parasitism (Lill 1999; Stireman and Shaw, Chapter "Natural History, Ecology, and Human Impacts on Caterpillar Parasitoids", this volume). How acoustical strategies (Yack, Chapter "Acoustic Defence Strategies in Caterpillars", this volume; Pierce and Dankowicz, Chapter "The Natural History of Caterpillar-Ant Associations", this volume) and chemical signaling to attract ants (Pierce and Dankowicz, Chapter "The Natural History of Caterpillar-Ant Associations", this volume) (and perhaps repel other predator types) change with instar is an area ripe for future research.

Consideration of the role of developmental stage is important because success prior to the pupal stage is a consequence of the cumulative demographic impacts of various ecological factors at all instars. Thus, a study that delimits the importance of an ecological factor for a particular instar may under- or overestimate the strength or totally overlook the impact of other factors at earlier and later instars. Our understanding of the factors that shape the ecology and evolution of caterpillars, their interactions with other trophic levels (Boege et al. 2019), and those factors that impinge on their ability to survive in a changing world would be incomplete if our studies are limited to a few developmental stages. A key first step in an important research program would be to document changes with instar by sampling species in individual clades or across the Lepidoptera tree of life. The next step would be to link such changes with changing selective pressures from one instar to the next.

Caterpillars in a Changing World

There is mounting evidence that entire communities of insects are under threat (Van Klink et al. 2020; Wagner 2020; Wagner et al. 2021). Studies of individual species of Lepidoptera across the years demonstrate that butterflies in particular can be critically threatened by habitat destruction (e.g., adonis blue butterfly: Thomas 1983; Palos Verdes blue butterfly: Arnold 1987; monarch butterflies: Brower et al. 2012). If this were not sufficiently alarming news, there is mounting evidence from across the globe that entire regional faunas are declining in some places (e.g., California: Forister et al. 2011; Great Britain: Warren et al. 2001). Salcido et al. (Chapter "Plant-Caterpillar-Parasitoid Natural History Studies Over Decades and Across Large Geographic Gradients Provide Insight into Specialization, Interaction Diversity, and Global Change", this volume and associated references) demonstrate declines in diversity of caterpillar genera at their Costa Rican wet forest site over the last 20 years. Accumulating sufficient data to show a decline at a regional level is difficult because natural fluctuations that are likely to occur in the absence of human intervention (Marquis et al. 2019a; Schowalter et al. 2021; Boege et al., Chapter "Impacts of Climatic Variability and Hurricanes on Caterpillar Diet Breadth and Plant-Herbivore Interaction Networks", this volume). Long-term data sets, like those described here (Braga and Diniz, Chapter "Trophic Interactions of Caterpillars in the Seasonal Environment of the Brazilian Cerrado and Their Importance in the Face of Climate Change", this volume; Boege et al., Chapter "Impacts of Climatic Variability and Hurricanes on Caterpillar Diet Breadth and Plant-Herbivore Interaction Networks", this volume; Salcido et al., Chapter "Plant-Caterpillar-Parasitoid Natural History Studies Over Decades and Across Large Geographic Gradients Provide Insight into Specialization, Interaction Diversity, and Global Change", this volume), are necessary to demonstrate statistically significant declines and discern their root causes.

All of the main interactions described in this book are potentially influenced by one or more factors driving global change. Uncovering the root causes for such declines, however, is exceedingly difficult because there are so many candidates (Wagner et al. 2021). The problem becomes even more knotty when one considers that climatic events (droughts, severe winter and dry seasons, late spring freezes) that cause local, temporary declines may actually be increasing in frequency because of human-driven climate change. One promising approach for better understanding the patterns and drivers of caterpillar abundance and phenology over large geographic scales is the analysis of data from citizen science projects such as iNaturalist and Caterpillars Count! (Hurlbert et al. 2019; Di Cecco and Hurlbert, Chapter "Caterpillar Patterns in Space and Time: Insights From and Contrasts Between Two Citizen Science Datasets", this volume). If the rate of accumulation of these data continues according to current trends, they will be a tremendous source of information regarding where and in what environmental contexts declines or phenological shifts are of greatest concern.

The consequences for such losses are potentially enormous. Just the loss of Lepidoptera alone would have a major impact on insect and overall biodiversity (Wagner and Hoyt, Chapter "On Being a Caterpillar: Structure, Function, Ecology, and Behavior", this volume). However, caterpillars, their pupae, and resulting adults (especially moths) provide major sustenance for insectivorous birds (Hurlbert et al. 2021), multitudes of rodent species, and the majority of the world's 11,000 species of bats. In addition, the vast diversity of hymenopteran parasitoids, likely the most species rich clade of the insect family tree, as well as the largest clades of dipteran parasitoids (Stireman and Shaw, Chapter "Natural History, Ecology, and Human Impacts on Caterpillar Parasitoids", this volume), predominantly rely on Lepidoptera larvae as a food source.

We end with a plea for the continued use of caterpillars as the subjects of both research and education, as well as for the necessary infrastructure for conducting such research and education. On the research side, continued documentation of the basic natural history of caterpillars, their host plants, and their natural enemies provides the information needed for understanding broad patterns of ecology and evolution, and our understanding of the growing human impacts on natural and managed ecosystems (Salcido et al., Chapter "Plant-Caterpillar-Parasitoid Natural History Studies Over Decades and Across Large Geographic Gradients Provide Insight into Specialization, Interaction Diversity, and Global Change", this volume). On the education side, teaching the life cycle of caterpillars in elementary school introduces children to the biology of insects, metamorphosis, comparative anatomy, biodiversity, and natural history (Clayborn et al. 2020). Teaching the same to adults reinforces messages learned earlier and provides an introduction to the diversity of the most speciose clade of macroscopic life on Earth. Both can lead to an increased appreciation of nature, which is so critical for support for conservation in an increasingly damaged world. Finally, it is important to recognize the critical role of museums and field stations for both research and education. Museums house voucher collections and are foci for education of the public. Field stations provide access to adjacent natural areas and basic laboratory facilities for caterpillar field research. Field stations also provide educational opportunities for students of all ages and all education levels. Together, these two forms of institutions facilitate the advances necessary for understanding the role of caterpillars in current and future ecosystems.

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