



# Monitoring tropical insects in the 21st century

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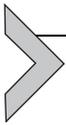
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## Abstract

Research has repeatedly shown that ongoing habitat loss and the increasing frequency of extreme climatic events have altered fundamental biological processes, threatening biodiversity and ecosystem functioning worldwide. However, the multitude of interacting factors underlying the impacts of these threats remain poorly understood in

tropical forests. This is unfortunate because the majority of terrestrial biodiversity resides in these habitats. The responses of organisms to environmental changes are often studied indirectly, for example, using discrete snapshots at different time periods at the same location. This is due to the challenges of compiling long-term data, especially for invertebrates. Evaluating how functionally important species assemblages will respond to anthropogenic threats requires continuous long-term monitoring. This is vital for arthropods because they are responsible for crucial ecosystem services and human food security. Here, we review existing arthropod monitoring schemes and consider some innovative avenues for future research that promise to improve monitoring of this important group in tropical systems.



## 1. Threats to insects in the Anthropocene

Recent reports suggest catastrophic declines in insect abundance with potentially dire implications for ecosystem functioning (Hallmann et al., 2017; Lister and Garcia, 2018; but see McGregor et al., 2019; Saunders et al., 2019; Willig et al., 2019). These declines mostly concern insect communities in temperate countries (Sánchez-Bayo and Wyckhuys, 2019), insect biomass in Europe and Puerto Rico (Dirzo et al., 2014; Hallmann et al., 2017; Lister and Garcia, 2018; Seibold et al., 2019), butterflies and moths in the United Kingdom (Long et al., 2016), insect pollinators worldwide (Goulson et al., 2015), or more generally the “associated biodiversity” that supports human food production through ecosystem services (FAO, 2014). In particular, pollinating insects have experienced significant declines for several decades in many parts of the world (Carvalho et al., 2013). This is a serious concern because pollination represents a critical ecosystem service (Garibaldi et al., 2013) and declines in pollinators have been directly linked with declines in the plants with which they interact (Potts et al., 2010). Most data indicating this decline originates from censuses of honeybee colonies and temperate bumblebees or from decreases in delivery of pollination services (Goulson et al., 2015). Case studies of wild pollinator population dynamics in tropical regions are rather infrequent and almost exclusively concern bees (Knoll, 2016).

The main threats to insect populations have already been identified. Habitat loss and fragmentation via agricultural expansion, land-use intensification and associated pollution (e.g. pesticides, light) are among the greatest threats to insects, causing population declines and shifts in community composition (Sánchez-Bayo and Wyckhuys, 2019). These threats are especially detrimental for endemic and specialized species that rely on specific host

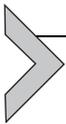
plants and/or habitats (Newbold et al., 2018). Intensive agriculture has also involved repeated or uncontrolled use of insecticides, such as neonicotinoids, which may have an impact on both target and non-target insect species (Forister et al., 2016). This insecticide use has been linked to population declines of economically important insects such as pollinators (Goulson et al., 2015; Sánchez-Bayo and Wyckhuys, 2019). Furthermore, the ongoing expansion of large-scale agriculture in the tropics may also negatively impact plant communities, shifting composition and altering the population dynamics of the insects feeding on them (Habel et al., 2019a). This is of particular importance, because most insects interact in some way with plants, and an estimated 85% of angiosperms, including most tropical tree species, are directly pollinated by insects (Ollerton et al., 2011). Most insect species are associated with living plants (Price, 2002) and are highly specialized in terms of food resources and microhabitats (Novotny and Basset, 2000). Hence, one of the greatest challenges facing modern agriculture is the development of low-impact, sustainable pest management and agriculture practices in order to promote more ecologically efficient food production (Laurance et al., 2014). In anthropogenically modified areas, ecologists have also shown that nocturnal pollination may potentially be disrupted by increasing light pollution, although this remains to be tested in tropical systems (but see MacGregor et al., 2015; Van Langevelde et al., 2017).

In addition to habitat degradation, climate change represents a considerable threat to insect communities (Chen et al., 2009; Deutsch et al., 2008). Globally, and for yet another year, 2018 was the warmest since records began (Cheng et al., 2019). In Central America, an increase in air temperature of 2–5 °C is expected by 2080 (Stocker et al., 2014). Extreme climatic events are also expected to occur with increasing frequency (Blunden and Arndt, 2017; IPCC, 2012, 2018; Ripple et al., 2020). While studies suggest that pronounced dieback may be triggered at 3–4 °C of global warming in Central American tropical forests (IPCC, 2018), there may catastrophic consequences for biomass productivity at just 1.5 °C increases (Lyra et al., 2017). These predicted changes may lead to local extinctions and/or alterations in the geographic distribution of species and hence, of local communities. Insects are particularly sensitive to climate change. This is in part due to their strong ecological links to plants; the slightest alteration to plant growth, abundance or phenology in a future disrupted climate can have severe consequences for associated insect communities (Pau et al., 2010, 2011). Individuals may either have to rapidly adapt or migrate in order to avoid

extinction, with changes in insect populations and distributions ultimately leading to alterations in ecosystem functioning (Kaspari et al., 2015; Thomas et al., 2004). However, our knowledge of insect responses to climate change is still limited (Hegland et al., 2009; Memmott et al., 2007). What we know is almost exclusively drawn from temperate systems (Sánchez-Bayo and Wyckhuys, 2019), and mainly relates to Lepidoptera (Altermatt, 2010; Diamond et al., 2011; McGregor et al., 2019).

Invasive species, and more broadly, changes in the distribution of pests and pathogens may also threaten insect populations, resulting in changes in ecosystem processes (Bohan et al., 2017a; Simler-Williamson et al., 2019; Yamamura et al., 2006). Changes in the populations of natural enemies, for example, are likely to have adverse effects on the regulation of primary consumers such as insect pests. Natural enemies provide a crucial service and their loss can be irreversible (Salcido et al., 2020) with negative consequences for human food security (FAO, 2014). Both insect pests and insect-spread pathogens can also negatively impact tree growth, causing mortality, altering forest structure and composition and potentially shifting ecosystem processes (Simler-Williamson et al., 2019).

The multiple interacting threats resulting from anthropogenic activities have negative consequences not only for insects themselves but also for the interacting species that rely on them. However, the responses of insects to anthropogenic threats are, even for common species, far from well understood in tropical ecosystems. In turn, long-term, continuous monitoring is urgently needed in tropical regions in order to test whether the results from studies in temperate systems showing dramatic declines in insect populations apply globally (Wagner, 2019).

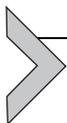


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## **2. Why monitoring insects is crucial in tropical ecosystems**

Tropical entomologists are in broad agreement that we have only quantified a small proportion of insect diversity (Stork, 2018). Understanding insect biodiversity in tropical ecosystems is of paramount importance for a number of reasons. First, insects represent the largest proportion of macroscopic terrestrial animal life, both in terms of species richness (Stork, 2018) and biomass (Pimentel and Andow, 1984). Second, the greatest diversity of both insects and the species with which they interact are observed in tropical rainforests (Basset et al., 2012). Third, insects play crucial roles in forest dynamics, through interactions such as herbivory, seed

predation, pollination, parasitism/mutualism, decomposition and nutrient cycling (Strong et al., 1984). Fourth, the ecosystem services that wild insects provide are of significant economic value, worth an annual estimated \$57 billion in the United States (Losey and Vaughan, 2006) and \$12 billion in Brazil (Giannini et al., 2015). Fifth, tropical insects may be particularly sensitive to global climate changes for several reasons: (1) The low seasonality of tropical regions is thought to result in evolution of insect species with narrower thermal limits (Kaspari et al., 2015). For example, tropical montane stream insects have a narrower thermal tolerance than temperate species, suggesting they will be particularly vulnerable to climate change (Polato et al., 2018). Projected air temperatures in the tropics appear to be close to the thermal limits of many insects, beyond which muscular coordination can be disrupted or lost (Deutsch et al., 2008). (2) Tropical insects are thought to be sensitive to desiccation and hence to drought or variation in rainfall. However, a recent study showed that canopy ants in tropical forest, when experiencing extreme temperatures have a more permeable cuticle that increases evaporative water loss making them more resistant to desiccation (Bujan et al., 2016). (3) Climate change may produce phenological mismatches with insect resources, such as host plants or prey (Facey et al., 2014; Singer and Parmesan, 2010). Only species that can track climate change by adjusting their phenologies to their resources will be able to persist under a changing climate (Cleland et al., 2012). This has been demonstrated mostly for temperate species whose host plants/prey are often only available seasonally but, to our knowledge, phenological mismatches due to climate change have not been studied in tropical forests.



### 3. Overview of insect monitoring programs in the tropics

In temperate ecosystems numerous long-term monitoring studies have been conducted and historical insect records have been compiled (Habel et al., 2019a), both over continuous time scales and using repeated snapshots with short time gaps (Augenstein et al., 2012; Hallmann et al., 2017; Wenzel et al., 2006). While this has helped to understand the responses of arthropod communities to land-use change and climate change (Sánchez-Bayo and Wyckhuys, 2019; Seibold et al., 2019; Wagner, 2019), the scientific rigour of such studies has been questioned (Leather, 2018; Thomas et al., 2019; Willig et al., 2019). In the tropics, the strongest long-term time-series data of insect species from a single location come from

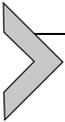
fruit-feeding butterflies (Grotan et al., 2012; Leidner et al., 2010; Srygley et al., 2010, 2014; Valtonen et al., 2013). These studies, performed in locations buffered from the effects of agricultural practices, do not suggest a decline in abundance, in contrast to those observations from temperate ecosystems. In fact, insect communities in tropical rainforests may actually be experiencing an initial positive effect of rising temperature (Basset and Lamarre, 2019). A study conducted in Panama on butterflies indicated that decreases in rainfall during El Niño events benefitted lianas. Consequently, lianas produced more leaves which led to an increase in the population sizes of the butterflies that feed on them (Srygley et al., 2010, 2014). However, a “concentration effect” may occur, where following the loss of suitable habitats elsewhere, populations concentrate into remaining favourable and less disturbed habitats (Spaniol et al., 2019).

Specialized interactions such as those between plants and their pollinators are particularly interesting study systems because phenological mismatch may occur (Vamosi et al., 2016). Roubik (2001) sampled euglossine orchid bees consistently between 1979 and 2000 in Panama in a relatively undisturbed forest. The assemblage showed no detectable change in diversity and no overall decline in abundance over the study period, but responses of individual species varied. Only 4 species declined, whereas 23 species remained unchanged and 9 species increased. These fluctuations appeared to be driven primarily by El Niño events, which produced a floral resource flush in the dry season, followed by an increase in bee populations (Roubik, 2001). A similar pattern has been found for nocturnal bees between 1977 and 1983 (Wolda and Roubik, 1986) with no directional changes in bee abundance but with fluctuations probably relating to seasonal flower abundance (see also Wolda, 1992). In Brazil, a study conducted on orchid bees for 7 years did not show any significant decline or any effect of climate anomalies on the assemblage (Knoll, 2016).

Other insect groups studied reveal varying patterns in the tropics. In French Guiana, Dejean and colleagues (2011) studied the responses of social wasps in plantations between 1997 and 2003. These authors found that recent climate fluctuations may have reduced the number of wasp colonies because of lowered wasp resistance to parasites and pathogens. Eleven years of monitoring tropical ants in an Ecuadorian rainforest revealed that overall community species richness remained relatively constant, showing a high temporal turnover of species but with no or only weak evidence of directional changes towards a new community (Donoso, 2017). In Borneo, neither abundance nor species richness of scarab beetle communities changed in

undisturbed forests between 1994 and 1999 (Kishimoto-Yamada and Itioka, 2013). On Barro Colorado Island (BCI, Panama), even small differences in the mean annual air temperature and precipitation (Anderson-Teixeira et al., 2015) appear to affect the populations of certain species of saturniid moths (Basset et al., 2017) and reduviid assassin bugs (Lucas et al., 2016) with contrasting directional responses among taxa on BCI (Fig. 1(7)).

Clearly, we currently lack sufficient insect monitoring data to either refute or support claims of global insect decline with respect to tropical regions (Janzen and Hallwachs, 2019). Our lack of knowledge concerning the response of tropical insects facing climate change and other major threats is in part due to lack of funding for long-term projects of this kind. We are not the first to note the challenge of finding support for long-term projects within the constraints of standard funding cycles. Our knowledge of the past, present and future directions of tropical insect populations depend greatly on ongoing support for taxonomists, museums and biodiversity studies. Therefore, because comprehensive data for tropical insects are lacking, caution is needed regarding extrapolations of temperate results to global scales (Simmons et al., 2019; Willig et al., 2019).

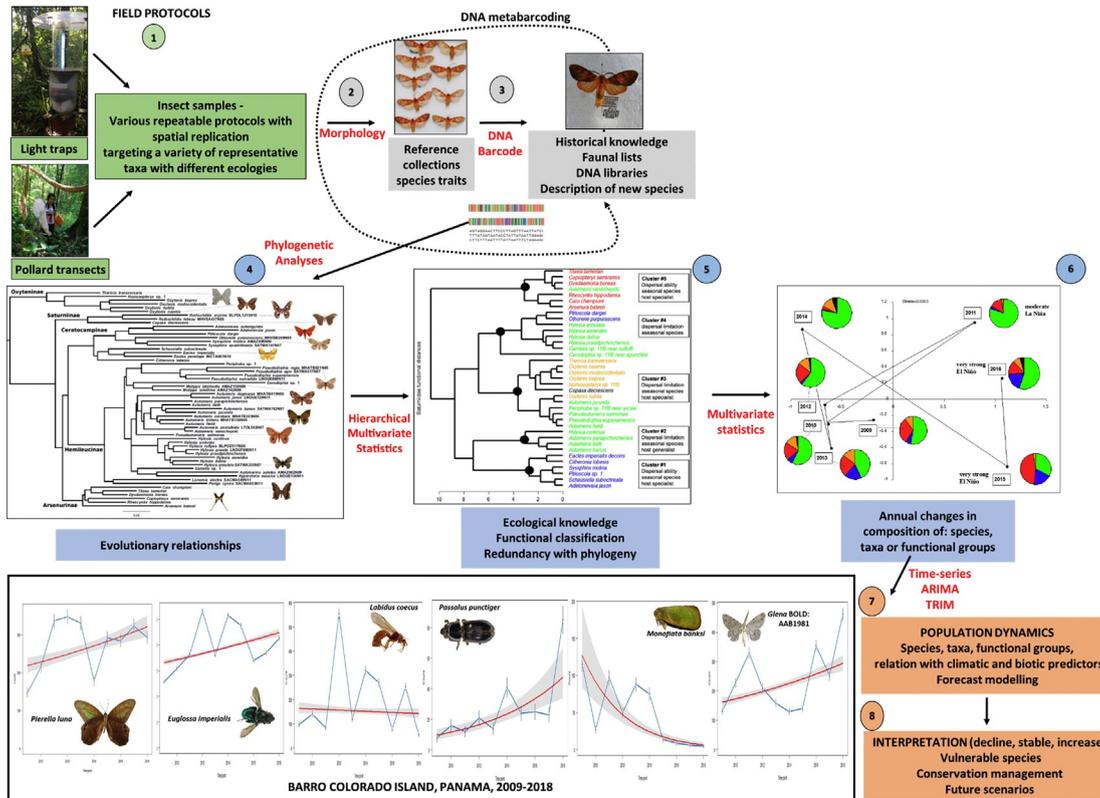


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#### **4. Case study: The ForestGEO arthropod initiative**

The ForestGEO Arthropod Initiative is an ongoing long-term monitoring scheme for tropical arthropods. The network of permanent forest dynamic plots monitored by the Forest Global Earth Observatory (ForestGEO) is an international collaborative network of scientists with 69 forest research sites across the Americas, Africa, Asia, Europe, and Oceania dedicated to advancing long-term studies in forest dynamics (Anderson-Teixeira et al., 2015). Within these forest plots each tree >1 cm DBH is tagged, identified and its DBH measured once every 5 years. This program provides a unique opportunity for long-term monitoring of insect populations and can capitalize on existing floristic, phenological and climatic data from these plots, thus simplifying efforts to study tropical insects and their interactions with plants (Godfray et al., 1999).

The ForestGEO Arthropod Initiative is currently monitoring focal arthropod groups at seven such permanent tropical plots. Here we present a case study of one of these sites, Barro Colorado Island (BCI) in the Panama Canal. The site receives an average annual rainfall of 2662 mm, with annual average daily maximum and minimum air temperatures of 31 and 23.6 °C, respectively. Since 1981 BCI has already experienced an increase of 0.36 °C



**Fig. 1** Workflow of the ForestGEO Arthropod Initiative monitoring scheme for long-term monitoring of population dynamics for common, poorly-known and species-rich insect assemblages. Modified from Basset, Y., Lamarre, G.P.A., Ratz, T., Segar, S.T., Decaëns, T., Rougerie, R., Miller, S.E., Perez, F., Bobadilla, R., Lopez, Y., Ramirez, J.A., Aiello, A., Barrios, H., 2017. The Saturniidae of Barro Colorado Island, Panama: a model taxon for studying the long-term effects of climate change? *Ecol. Evol.* 7 (23) 9991–10004, <https://doi.org/10.1002/ece3.3515> and Basset and Lamarre (2019).

in mean annual temperature and a 17.9% increase in mean annual precipitation (Anderson-Teixeira et al., 2015). The principal objective of the ForestGEO Arthropod Initiative is to detect long-term changes in the abundance and composition of focal assemblages of arthropods, driven primarily by climatic cycles and changes, as opposed to short-term stochastic changes (Basset et al., 2013, 2017). Initiated in 2009, the field protocol enables the quantification of population dynamics for 19 focal arthropod taxa including 10 Lepidoptera taxa, both diurnal (Hesperiidae, Riodinidae, Nymphalidae, Pieridae, Papilionidae, Lycaenidae) and nocturnal (Saturniidae, Geometridae, Arctiinae, Pyraloidea); 3 Coleoptera taxa (Dynastinae, Passalidae, Platypodinae); 2 Hemiptera taxa (Flatidae, Reduviidae); 2 Hymenoptera taxa (Euglossini, Halictidae) and 2 social insect taxa, ants and termites (including workers and alates; see Box 1 for a

### **BOX 1 Monitoring social insects in the tropics.**

Social insects represent core ecological components of ecosystems, with high biomasses, particularly in the tropics. They drive ecosystem processes such as pollination (bees, wasps), predation (ants, wasps), soil turnover (termites, ants), seed dispersal (ants), and decomposition (termites). As with other tropical arthropods, they experience a range of anthropogenic threats, which are expected to alter the ecosystem processes that they mediate. Hence, long-term monitoring of social insect populations and communities is vital. However, monitoring of social insects involves some considerations that do not apply to the usual methods used for monitoring of solitary organisms. In order to facilitate inclusion of social insects into long-term monitoring programs for tropical arthropods, we discuss these considerations here.

#### *Which considerations are specific to monitoring social insects?*

Social insects operate from colony centres that move relatively infrequently. In this sense, social insects are similar to plants (Andersen, 1991), as they represent spatially stable colonies, each using resources in the local area and disseminating propagules to reproduce (winged reproductives for social insects, seeds for plants). These propagules then experience strong competition from nearby colonies while trying to initiate a new colony. Hence, the success of long-term monitoring programs for trees, for example the ForestGEO network (Anderson-Teixeira et al., 2015), should be an inspiration for long-term monitoring of social insects. For ants and termites, presence of a wingless worker means that a colony has successfully established in the local area, within close distance of the sampling point. As a caveat, the limits of mobility for entire colonies of social insects are poorly-known, and colony monitoring of species with high

*Continued*

### **BOX 1 Monitoring social insects in the tropics.—cont'd**

colony mobility may not reflect colony mortality. For example, species nesting in ephemeral habitats, such as ants living in small dead twigs, appear to move more frequently than those in more permanent habitats (Byrne, 1994), and hence the latter should be targeted for long-term colony monitoring in the tropics. Furthermore, presence of colonies does not necessarily mean that there is successful reproduction occurring, and hence long-lived but non-reproductive colonies might be misinterpreted as representing healthy populations. This issue could be avoided by monitoring population structure (i.e. abundances of colonies at different life stages), rather than just recording the presence of individuals. Light trapping for reproductive individuals should also be included to help overcome this issue.

#### *Sampling design and statistical analysis*

Sampling methods used for social insects can either be based on whole colony sampling or sampling of individual workers. Intensive methods that involve searching for colonies can be considered to create a long-term scheme to parallel that used in permanent vegetation plots (Anderson-Teixeira et al., 2015). If this is not practical (e.g. cryptic nests that are difficult to survey in rainforests), then a scheme based on sampling individual workers should be considered (e.g. Winkler leaf litter sifting). However, individual workers from a single sample cannot be considered as independent data points, since they are all likely to come from a single colony. One method to overcome this is to use presence-absence data for analyses (Agosti et al., 2000). Such data can be considered to relate to colony densities if distances between sampling points are sufficient to prevent a single colony from foraging at multiple sampling points. Hence, spatial arrangement of sampling points should take into consideration foraging ranges of the group. Statistical methods appropriate for presence-absence data should then be used. These include, diversity indices such as species richness, indices for differences in composition between samples such as Sorensen's index (Fayle et al., 2010), incidence-based species richness estimators such as ICE or Chao 2 (Longino, 2000), Generalized linear models with binomial errors for presence/absence of individual species, or Poisson errors for species counts. Abundances of social insects may still be worth recording, since abundance and biomass are likely to reflect the degree to which they are able to mediate ecosystem processes. Abundance at baits can also give insights into behavioural dominance of different species (Drescher et al., 2011; Dworschak and Bluethgen, 2010). Finally, since the objective of monitoring (of communities) is to reliably capture as many species in the community as possible, optimisation studies can be carried out. These allow selection of particular combinations of sampling methods to ensure that the greatest number of species is collected given the resources available (Yusah et al., 2012).

discussion of considerations relating to monitoring social insects). All field protocols targeting the above-mentioned taxa are standard, reproducible entomological methods (Basset et al., 2015) that reflect real population changes rather than changes in insect activity (Basset et al., 2013). To date, the ForestGeo Arthropod Initiative at BCI has recorded more than half a million specimens representing over 2300 focal species. The initiative has accumulated 11 years of continuous data, including four seasonal replicates per year, so that time-series to date include more than 40 data points. In Fig. 1, we describe the general workflow of the monitoring components with time-series examples for common species (Basset and Lamarre, 2019).

Our first attempt at understanding climate-driven changes in tropical insects focused on saturniid moths of BCI, Panama (Basset et al., 2017; Box 2). Our data on species abundance and composition suggested that the year 2011 (a weak-to-moderate La Niña resulting in increased rainfall) was different from other years, with distinct peaks in populations for six of the 14 saturniid species studied (see also Box 2). The number of saturniid species with peak in abundance for each sampled year appeared to be related to the magnitude of these anomalous events (La Niña, El Niño), which was also reflected in changes in faunal composition.

These continuous long-term datasets are crucial for two reasons: (a) because continuous or frequent monitoring (as opposed to resurveys or snapshots at longer time periods; see Chen et al., 2009; Colwell et al., 2008; Donoso, 2017) is critical to measure annual change in insect populations, to evaluate the main drivers of arthropod responses to climate changes and anomalies, and to estimate the detection probability of vulnerable and resilient species (Basset et al., 2017; Newbold et al., 2018; Roubik, 2001) and (b) because tropical insects often exhibit short generation times, these data already potentially represent a significant number of generations (as low as eight generations per year for some insect pests; Nair, 2007). This contrasts with plant monitoring, where for some taxa monitoring schemes still cover much less than the time of a single generation.

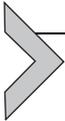
The ForestGEO Arthropod initiative proposes a comprehensive framework that we hope will serve as a baseline study to be replicated at other monitoring sites. Because it would be unrealistic to monitor all taxa in tropical forests, we explore three different approaches to the selection of indicator taxa that may be highly sensitive to climate changes but are still representative of many insect species sharing taxonomical (Fig. 1(3)), evolutionary (Fig. 1(4)) or functional relationships (Fig. 1(5)). The workflow includes exploration of the temporal dynamics of tropical insect

## **BOX 2 Functional traits of tropical moths and climate change: an example.**

Saturniidae (Lepidoptera) are an interesting model taxon in comparison to other insect groups since the adults do not feed, have short life spans, and, particularly for the heavy-bodied species, are unable to fly until their thoracic muscles have reached a temperature of 35 °C, achieved by muscular ‘shivering’ (Blest, 1960). For saturniids, rising air temperature means allocating less time to shivering and more time to finding mating partners and searching for suitable oviposition sites. Warming may represent a significant advantage for species with particularly short adult life spans (Janzen, 1984). For an 8-year period (2009–2016), we analysed population dynamics of saturniid moths on BCI and tested the importance of using functional classification in climate change studies (Basset et al., 2017). First, we generated a morphological and life-history traits-by-species matrix from collected specimens to compute a principal component analysis (PCA) prior to the construction of the functional hierarchical classification. Second, the different components (axes) of the PCA were used as combinations of traits to define a Euclidean functional space with reduced uncorrelated dimensions, where each species is represented by its PCA axis scores (Hawking and New, 2002). This approach is an efficient way to produce high quality functional spaces where the weight of each synthetic trait is relevant to the fraction of the total trait variance it explains (Basset et al., 2017; Maire et al., 2015). Then, we computed the complete functional classification using hierarchical *daisy* clustering methods based on functional clusters defined by the saturniid species scores on all axes (Fig. 1(5)). By exploring the functional space of these tropical moths, we showed that the species sharing life-history traits related to dispersal (body size), annual seasonality (phenology), and host plant specialization (plant use) can be clustered into five distinct functional groups (Fig. 1(5)). The use of the functional traits also revealed that tropical saturniids display contrasting functional attributes and that the functional groups exhibit different directional responses, possibly related to climate changes or extreme events (such as in the years 2011 and 2015). Species belonging to one distinct functional group, including large species with good dispersal ability, high host specialization and high seasonality, collectively showed a significant moderate increase over time. We speculate that this may form the basis for explaining the positive effect of rising air temperature on certain saturniid populations (Basset et al., 2017). Moreover, our results also emphasize the need to study below the species level and start exploring intraspecific responses in tropical insects that may provide clues about future adaptation and local responses. The use of functional traits and groups over taxonomic categories may also improve our ability to interpret complex results when confronted with diverse groups such as tropical insects. Furthermore, this simplification is potentially useful when dealing with a multitude of species, in order to present more succinct results to the general public and decision-makers.

communities (Fig. 1(6)) and the directional responses of contrasting trophic groups (related to their function in ecosystem processes) to climate changes and anomalies (Fig. 1(7)).

Finally, the initiative hopes to deliver an easily-interpretable synthesis of the future scenarios for tropical insect communities in order to encourage the rapid adoption of conservation measures for vulnerable species and their habitats (Basset and Lamarre, 2019; Fig. 1(8)). In the next section, we discuss some innovative avenues for future research that promise to improve arthropod monitoring in tropical systems.



## **5. Addressing present and future challenges in monitoring tropical insects**

### **5.1 Inclusion of functional traits in monitoring programs**

Traditional community ecology uses the identity of species to understand how changes in habitat condition influence community composition and structure. This approach, however, has its limitations. Critically, the biology of a given species is often unknown and, especially in tropical regions, many species remain undescribed (Basset et al., 2012; Stork et al., 2015). The use of functional traits has been well established in community ecology, because unlike species identities, functional traits are related to species performance and ecosystem processes (McGill et al., 2006; Weiher, 2011). Measurement of functional traits allows inferences to be made about a species' role in the ecosystem, without prior natural history knowledge. However, ecological traits related to a species' function in the ecosystem are numerous and the choice of which functional traits to include should be made based on the underlying mechanisms that constrain species performance and influence ecosystem processes (Weiher, 2011). Moretti et al. (2017) summarized 29 functional traits that can be measured for terrestrial invertebrates and are categorized into 5 types: morphology, feeding, life history, physiology and behaviour.

Functional traits are now increasingly being included in studies of species' response to climate change. Most morphological traits can be measured a posteriori using preserved specimens collected from previous surveys or monitoring. Other functional and life-history traits, such as feeding guild, clutch size, and life span, may be obtained from existing literature if the biology of species is well known, although such information is unlikely to be available for most tropical biota. However, most functional traits related to physiology (e.g. metabolic rate) and behaviour

(e.g. activity time and locomotion speed) require live specimens. Hence such traits must be selected a priori before monitoring starts (e.g. increase in metabolic rate with increasing temperature, [Dillon et al., 2010](#)). Continuous traits are measured from a number of individuals of the same species and average values are used for analysis. Intraspecific variation is common but generally of smaller magnitude than interspecific variation ([Weiher, 2011](#)).

Intraspecific changes in functional traits should be monitored through time, accounting for other factors such as genotypic variation, phenotypic plasticity, acclimation and ontogeny ([Weiher, 2011](#)). Morphological traits such as body size ([Fontanilla et al., 2019](#)) and body colour ([Dalrymple et al., 2017](#); [Xing et al., 2018](#)) can be easily measured. These traits are interpreted as phenotypic correlates of functional attributes ([Weiher, 2011](#)). For example, temperature generally decreases with increasing elevation, and ectotherms at higher elevations need to become efficient in gaining heat while minimizing heat loss. [Bishop et al. \(2016\)](#) investigated body colour and body size of ant assemblages along elevational transects and found that ants became darker (to maximize heat gain) and larger (to minimize heat loss) with increasing elevation. A recent study on butterflies also suggests that univoltine butterflies are less sensitive to climatic extremes than are multivoltine species ([McDermott et al., 2017](#)), emphasizing the importance of including life-history traits in studies related to climate change. Species that share similar functional attributes (not necessarily those that are closely phylogenetically related) may have similar responses to climate fluctuations and anomalies, and these responses may be easier to interpret than more traditional species-specific approaches ([Didham et al., 1996](#); [Valtonen et al., 2013](#)). In temperate systems, functional categories have been used for Lepidoptera as relevant surrogates for life-history changes induced by climatic shifts ([Pau et al., 2010](#)). Within the context of climate change, it is therefore necessary to identify the key functional traits associated with mechanisms by which single species or groups of species influence ecosystem properties ([Lavorel and Garnier, 2002](#)). However, in the tropics, where the knowledge of life-history traits is limited, relevant species traits have often been limited to a few taxa, such as butterflies or ants ([Diamond et al., 2011](#); [Slade et al., 2013](#)).

Therefore, compiling records of functional traits and life-history traits, sharing databases publicly and initiating large-scale collaborations among tropical, behavioural, evolutionary, ecological, and physiological entomologists is a fruitful future research direction.

## 5.2 Inclusion of tolerance to temperature and desiccation in monitoring programs

Ectotherms are particularly sensitive to changes in environmental temperatures and precipitation patterns as many of their physiological functions are influenced by temperature and water balance (Benoit and Denlinger, 2010; Deutsch et al., 2008; Easterling et al., 2000; Paaijmans et al., 2013). A growing body of research relates to determining the tolerance of ectotherm species, including insects, to changes in temperature and desiccation risk (Pinsky et al., 2019, Terblanche et al., 2011, 2017).

Changes in temperature can affect an insect's phenology, geographical distribution and performance (Deutsch et al., 2008). One common physiological measurement consists of experimentally quantifying the critical thermal maximum (CT<sub>max</sub>) and minimum (CT<sub>min</sub>), the temperatures at which an ectotherm loses motor control or locomotion (Bujan et al., 2016; Kaspari et al., 2015, 2016). This information is vital to understand the energy and the (future) cost allocated to thermoregulation among functionally important species in tropical forests. Work performed by García-Robledo et al. (2015) in Costa Rica focused on thermal tolerance in rolled-leaf beetles along a tropical elevational gradient. Leaving beetles in falcon tubes in a water bath to measure CT<sub>max</sub>, these authors observed that species at low elevations are more tolerant to high temperature than those at mid and high elevations. A similar methodology was used to determine the difference in thermal tolerance between nocturnal and diurnal ants in Mexico (García-Robledo et al., 2018). The authors demonstrated that ants from tropical rainforests show lower tolerances to high temperatures than those from semi-desert and subtropical dry forests. Kaspari et al. (2015) showed that CT<sub>max</sub> and desiccation resistance are inversely related in canopy ants, but positively correlated in understorey ants, that larger ants have broader thermal tolerances than smaller ants, and that canopy nesting species are less sensitive to temperature, supporting the thermal adaptation hypothesis (Bujan et al., 2016; Kaspari et al., 2015, 2016). Ideally, insect physiological traits for species that are part of long-term monitoring programs should be measured under manipulated air temperature and humidity based on projected climate scenarios (IPCC, 2018). For example, the lower and the upper critical temperatures (CT<sub>max</sub> and CT<sub>min</sub>) of larvae and adult insect species across a range of temperature and humidity conditions could be determined using thermo-incubators. In turn, these data may help to refine functional classification and the predictive time-series models and evaluate how species

will cope with climate change in the future and their risks of extinction. For example, we would expect that species that are already close to their upper thermal limit would experience negative impacts on their populations as a result of increases in temperature due to climate change.

### 5.3 Long-term monitoring of interaction networks in tropical ecosystems

There is increasing understanding regarding the responses of interaction networks to both anthropogenic and non-anthropogenic environmental factors, for example changes with altitude (Maunsell et al., 2015; Morris et al., 2015; Plowman et al., 2017), latitude (Dalsgaard et al., 2011; Forister et al., 2015), habitat fragmentation (Emer et al., 2013), and habitat conversion (Tylianakis et al., 2007). Although this information is valuable, there remains no long-term program monitoring network structure changes in the tropics, despite calls for such projects (Kaiser-Bunbury and Bluthgen, 2015).

Because of the lack of long-term monitoring data, we must extrapolate from responses of networks to existing gradients of climate and anthropogenic habitat modification. This is vital because many aspects of ecosystem functioning are mediated through interactions, and hence network structure can affect ecosystem processes (Poisot et al., 2013). Furthermore, understanding network structure can give insights into ongoing ecosystem stability, because network structure can predict impacts of cascading extinctions (Dunne et al., 2009), for example, through identification of keystone species (Ebenman et al., 2004). Many existing studies relate to changes in host specificity along environmental gradients and can provide clues to climate change related network responses. These shifts in specificity can be driven to a great degree by the well-known large-scale changes in species richness, the most comprehensively studied of which being tropical-temperate latitudinal differences. For example, parasitoid networks do not vary with latitude, in any of a range of specificity metrics, once variation in host diversity is accounted for (Morris et al., 2014). A similar pattern of increased numbers of interactions with lower-level species by each higher-level species is observed for bird-plant frugivory networks, in which birds are less specialized in the tropics, because there are more available fruit species to feed on there (Dalsgaard et al., 2017). Such patterns are also observed in relation to altitude; for both herbivore-parasitoid networks (Maunsell et al., 2015), and mutualistic symbiotic ant-plant networks (Plowman et al., 2017) reduced host diversity results in reduction in generality with increasing altitude.

Hence, changes in the diversity of lower-level species in trophic networks are likely to be an important driver of overall network structure (Pellissier et al., 2013). For systems in which long-term monitoring indicates reductions in species richness, we would hypothesize that this will result in increases in the level of observed specialization.

However, all of the above-mentioned studies rely on snapshots of network patterns at single points in time, and hence long-term impacts of environmental changes on network structure are likely to be missed. An understanding of how interaction networks respond to different kind of threats (land-use change, including habitat fragmentation, and climate anomalies) and how these responses vary between network types (e.g. pollination, parasitoidism), is urgently needed if we are to mitigate against irreversible impacts.

#### **5.4 Evolutionary drivers of network re-wiring in the face of climate changes**

Species are not independent data points (Harvey and Pagel, 1991) and often share functional similarities with their relatives (Wiens et al., 2010). It is important to account for these phylogenetic patterns as part of monitoring schemes. Species level relationships are being increasingly well estimated through the use of sequence data and the construction of phylogenetic hypotheses. For example, grafting methods linking shallow sequencing (e.g. COI for insects) to multigene datasets increase connectivity for understudied tropical groups (Basset et al., 2017; Chesters, 2017). Armed with phylogenies, researchers can harness the predictive power of trait conservatism, ideally in combination with detailed functional measurements with which to qualify this assumption. Basic quantification of phylogenetic signal in species extinction risk over time, for example, can help to identify lineages pre-disposed to local extinction when monitoring data are comprehensive enough (Basset et al., 2015). Moreover, we can predict species' responses to climate and habitat change, tease out key traits or even map the response of local species to invasive ones (Pearse and Altermatt, 2013). This approach is critical as we race to understand the loss of species that may not even have a name yet (centinelian extinction), let alone an entry in a functional database. Extrapolating species level responses or their position in a network based on phylogenetic and trait data (Segar et al., 2017) also allows us to understand the eco-evolutionary drivers of network re-wiring in the face of global change. There are several predictive approaches currently available to researchers.

Phylogenetic Generalized Linear Mixed models (PGLMMs) (Ives and Helmus, 2011; Pearse et al., 2015) and Generalized Estimating Equations (Paradis and Claude, 2002) offer an extremely flexible framework for use in tropical arthropod monitoring schemes because they can both quantify the role of phylogenetic, functional and temporal correlations. Bayesian implementation of generalized mixed models is similarly promising and flexible (Hadfield, 2010). We anticipate that machine learning (e.g. phylogenetic ‘Flexible Discriminant Analysis’, phyloFDA) will provide exciting opportunities for fully predictive network and species level approaches for interrogating monitoring datasets (Motani and Schmitz, 2011; Pichler et al., 2019). Scripts for these analyses should be user friendly for local stakeholders and embedded in an accessible workflow. In combination with increasingly automated monitoring and molecular identification tools (Bohan et al., 2017a; Keck et al., 2018) a predictive phylogenetic framework will help to understand both historical responses and forecast future trends in the Anthropocene.

## 5.5 Developments of high-throughput DNA sequencing technologies

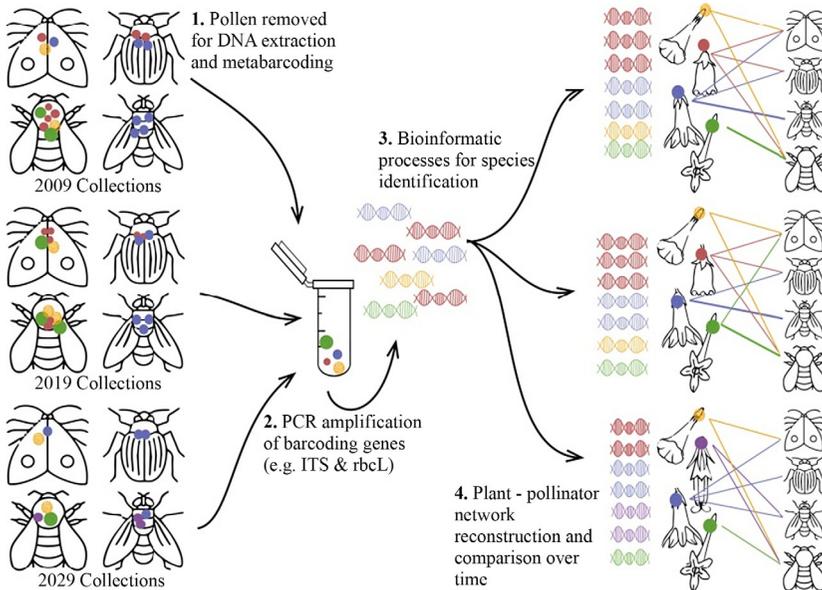
Beyond phylogenetic relationships between species, documenting changes over time has been a central goal of evolutionary biology, particularly when studying genetic responses of species to environmental change (Wandeler et al., 2007). Often, these studies depend on present day genetic snapshots with little room for manipulation beyond common garden or translocation experiments, or studies performed in controlled laboratory conditions (Flanagan et al., 2018). The use of natural history collections (Bi et al., 2013) or long-term monitoring programs (Silvertown et al., 2006) allows researchers to extend the temporal scale that these studies encompass. This enables them to identify periods of loss of genetic diversity, reductions in effective population sizes, changes in gene flow patterns and even measure rates of introgression from non-native introductions to native populations (reviewed in Wandeler et al., 2007).

High-throughput DNA sequencing technologies now allow for extending these studies to much larger scales, both in terms of genomic regions and numbers of samples, at rapidly decreasing costs and for non-model organisms. Even though many of these historical long-term collections were not done with genetic studies in mind, some sequencing techniques are able to retrieve meaningful data even from low quantities of degraded DNA (Staats et al., 2013). The continued developments in preservation of field

samples, now with DNA studies in mind, has set the stage for genetic monitoring as a way of studying population changes, particularly during this period of extreme anthropogenic environmental change (Flanagan et al., 2018; Schwartz et al., 2007). For instance Dormontt et al. (2014), using historical and contemporary collections, were able to reconstruct the invasion history of *Senecio madagascariensis* in Australia since its introduction in 1918. There was also an increase in genetic diversity, likely resulting from a second introduction event sometime during the 20th century. This resolution would not be possible from surveying present day samples alone, highlighting the importance of historic collections and long-term monitoring programs (Dormontt et al., 2014). Similarly, the level of detail from high-throughput sequencing technologies continues to increase allowing us to characterize species interactions, as is the case with network reconstructions based on DNA metabarcoding (Gous et al., 2019).

Historic collections and those from long-term monitoring not only record the time and place of individual collection, but may also include information regarding their host plant association and surrounding habitats. For example, pollen carried by flower-visiting insects can be used to identify recently visited flowers, giving us an indication of plant community structure and visitation rates (see Fig. 2). Gous et al. (2019) used this approach by applying DNA metabarcoding to pollen extracted from South African bees sampled over a 93-year period. Although taxonomic resolution was generally low (we lack a plant universal barcode with comparable species level resolution to COI), the authors were able to identify the pollen carried by these bees to genus level and were even able to identify plant taxa that were not listed regional databases (Gous et al., 2019). Genetic methodological, technological and statistical techniques continue to develop for the study of taxonomical, functional and evolutionary responses of terrestrial biodiversity to climate-driven changes.

Overall, new molecular methods such as DNA metabarcoding are very promising for the elimination of taxonomic barriers allowing biological monitoring at low cost (Yu et al., 2012). Such methods are especially urgent for highly diverse tropical forests. Metabarcoding represents a powerful and less labour-intensive approach for the detection and monitoring of indicator species and functionally important groups (Basset et al., 2017; Beng et al., 2016). This approach aims to compare the occurrence of these groups over time to study their response to environmental changes and climatic anomalies. For example, adult moths associated with flowering plants can be sampled using light traps and have the potential to be routinely identified using



**Fig. 2** Reconstructing pollination networks from monitoring and/or historic collections. Pollinating insects often carry a snapshot of the plant community they visited at the time of capture. Pollen DNA metabarcoding techniques allow researchers to extract pollen DNA from individuals and amplify standard barcoding genes. High-throughput sequencing can generate millions of short reads which can be sorted to high taxonomic resolution and used to reconstruct pollination networks from the sampled individuals. Depending on the timespan of these monitoring efforts, researchers can potentially identify floral resource use by pollinators over different sampling periods (i.e. different seasons) and even trace the re-wiring of these networks due to alien plant introductions or loss of native species.

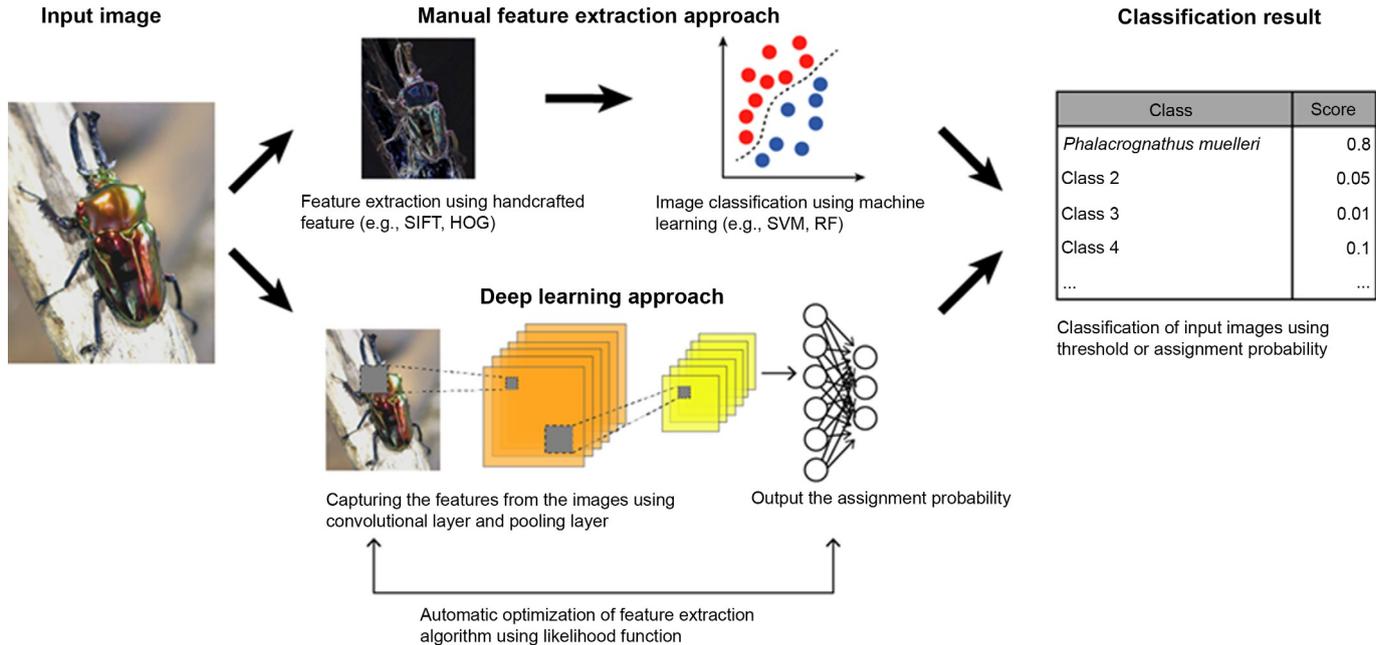
new molecular methods (Ji et al., 2013). The ForestGEO Arthropod Initiative (see above) seeks to implement and replicate new monitoring protocols for tropical insects based on molecular techniques at other monitoring sites (see Tang et al., 2015) and to thus explore the utility of metabarcoding in long-term monitoring. However, one of the first challenges ahead, prior to extending the use of metabarcoding in further monitoring sites, is to obtain clean, complete DNA barcode libraries for these focal tropical taxa, because results from metabarcoding studies are highly dependent on database quality.

## 5.6 Machine learning

Image recognition and classification techniques have made advances that hold promise for monitoring of tropical arthropods. Image-based species

identification technology has progressed as a result of the development of computer vision technology. Computer vision works by enabling computers to see, identify and process images in the same way that humans do (Szeliski, 2010) using machine learning. Computer vision machine learning approaches can be categorized as being both (1) manual feature extraction and (2) deep learning (Fig. 3). The manual feature extraction approach consists of two phases: feature extraction and classification. In the feature extraction stage, features of the classification target in the image are extracted based on pixel values. The classification stage is used to calculate the probabilities of each image belonging to a range of classes, in this case species, or higher-level taxa. Common classification methods include machine learning algorithms such as Support Vector Machines (SVM), Random Forest (RF) and Artificial Neuronal Network (ANN).

Feature extraction aims to extract the target object accurately from images. However, development of these algorithms is still challenging and often present problems specific to the kinds of objects being identified. In the past, manually deriving characteristic features was the main method used. Generally, object feature description methods can be categorized as using either global features or local features (Martineau et al., 2017). Early research on insect recognition used global features based on colour, texture or geometric invariants, such as colour histograms, geometric shape (eccentricity, perimeter, area, etc.), or other relatively simple features (Liu et al., 2016). However, because simple features are very sensitive to rotation, scale, translation, and viewpoint changes, this classification method did not work well on objects with large intraspecific variation or high interspecific similarity. Moreover, these methods are often labour intensive because they require manual image manipulation in order to identify key features. To address this issue, researchers began using local feature-based representation of insect images, which allows learning with much less direct user interaction (Cheng and Geyer, 2012; Solís-Sánchez et al., 2011; Venugoban and Ramanan, 2014). The most popular of these local feature-based methods employ custom features, which are feature extraction algorithms such as Local Binary Patterns (LBP; Ojala et al., 2002), the Scale Invariant Feature Transform (SIFT; Lowe, 2004), Histogram of Oriented Gradients (HOG; Dalal and Triggs, 2005). For example, a local feature-based insect identification scheme using the SIFT descriptor to classify five common pest species in orchard habitats achieved 88.4% accuracy (Wen et al., 2009). A hierarchical combination model based on local feature and global feature models was able to classify eight insect species with accuracy of 86.6% (Wen and Geyer, 2012). However, these approaches require careful choice of



**Fig. 3** Schematic diagram of computer vision machine learning pipeline for image-based species identification. In the manual feature extraction approach, image classification is performed by machine learning based on algorithms (e.g. handcrafted feature) designed by domain experts. On the other hand, in deep learning approach, convolutional neural networks automatically extract the feature and developing a robust classification model by learning a training data.

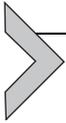
features, and a sophisticated design for the preprocess procedure (i.e. ways to aggregate them). Additionally, for many features it has not been possible to extract them manually in the past (Wäldchen and Mäder, 2018).

Recently, deep learning based approaches have allowed the construction of sophisticated recognition systems. Deep learning (DL) is a specific kind of machine learning and it builds upon ANN. DL can simultaneously optimize the feature extraction stage and classification stage through during the learning of training images. A strong advantage of DL is automatic feature learning; the method uses training data to categorize image content without a priori specification of image features (LeCun et al., 2015). Recently, DL has been employed in ecological studies (e.g. Carranza-Rojas et al., 2017; Norouzzadeh et al., 2018) and insect classification studies (e.g. Liu et al., 2016; Thenmozhi and Reddy, 2019). Liu et al. (2016) classified 12 species of paddy field pest insects with greater than 95% accuracy. Thenmozhi and Reddy (2019) combined DL and transfer learning for classification of 40 crop pest species and achieved over 90% accuracy. How these methods can be scaled-up to species-rich assemblage remain to be tested.

In addition to these developments in software, there are now massive repositories of ecological image data uploaded from field-based cameras or captured by citizen scientists available to implement public monitoring programs and for ecological analysis. For example, to date iNaturalist has archived 29 million images of 244,183 species taken by citizens and researchers (iNaturalist.org, 2019). Furthermore, some natural history museum collections have been digitized, which has resulted in large and historically relevant digital datasets. For example, the iDigBio portal currently provides more than 1.8 million georeferenced images of vascular plant specimens (Willis et al., 2017). Such large image datasets in combination with the recent advances in machine learning based-image recognition and classification technologies are bringing image-based species identification and its application for ecological monitoring closer to reality (Wäldchen and Mäder, 2018; Weinstein, 2017).

Machine learning can potentially identify the taxa of specimens prepared from ongoing monitoring programs. Such specimens are usually stored in boxes and therefore images can be obtained in bulk (i.e. capturing the image of all specimens in a specimen box). Alternatively, images of live specimens can be captured in the field by entomologists (e.g. capturing the images of insects on the white sheet of the light trap) or by the many scientists and other people around the world that carry a smartphone with a high-resolution camera. However, there remains the question as to what level

of accuracy (correctly identifying specimens) and precision (taxonomic resolution) machine learning can achieve in monitoring programs. [Martineau et al. \(2017\)](#) surveyed 44 existing image-based insect classification publications and found that laboratory photography of insects is still the most widely used method, with positioning of insects being carried out manually in most cases. [Martineau et al. \(2017\)](#) also pointed out that there is still little work being done to develop insect identification systems that can be used in the field rather than in the laboratory. To evaluate the utility of image-based species identification techniques for insect monitoring, further research based on images taken in the field is necessary.



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## 6. Conclusion

Current incentivization in modern agriculture encourages habitat loss, fragmentation and the use of herbicides and pesticides, all of which represent threats to insects. Extreme climate events, invasive species, pests, and pathogens are also threatening local insect populations and causing changes in ecosystem processes. However, species responses to individual anthropogenic threats in tropical regions are not yet well understood, mostly because we lack adequate monitoring schemes. Despite their ecological and economic importance, insects are still underrepresented in scientific research, leading to potential bias in our understanding of the functional ecology of ecosystems. The dramatic decrease in funding studies related to biodiversity science has also resulted in a lack of training, leading to a decrease in fundamental and applied knowledge in entomology. The public should be educated about the importance of insects ([Lamarre et al., 2018](#)). We need a bio-literate society that protects insects to ensure humanity's own survival ([Basset and Lamarre, 2019](#)).

This review highlights the fact that insects may be particularly sensitive to climate changes and so deserve more attention. Only continuous long-term monitoring will enable us to understand insect population dynamics in the face of future climate-driven changes. Functional traits can be used to delineate key functional arthropod taxa in tropical forests. Those focal insects (herbivores, pollinators, predators, social insects) need to be monitored in long-term programs using reproducible, standardized field protocols. This approach can then be proposed to stakeholders, cities and national parks, leading eventually to key insights into the conservation of vulnerable species and habitats. However, much work is needed to achieve this final goal. For example, we need to determine the tolerance of tropical ectotherms,

including insects, to future changes in temperature and humidity and to know which species or functional groups are vulnerable to extinction. We also need to generate time-series across multiple sites and forecast models of insect assemblages to understand their future directional changes and to define early warning systems of the health of tropical forests. More work is also needed in distinguishing between directional changes and background variation in communities, and the nature of climate change events and their impacts on terrestrial ectotherms at various spatial scales (e.g. involving collaboration with climate scientists). More collaborative cross-disciplinary projects focused on protecting insect populations are vital to mitigate potential disruption or loss of the important ecosystem services they provide. Given current expectations of warming and an increased frequency of extreme weather events (such as the Amazonian and Australian fires of 2019 and 2020) these actions are urgent.

Exciting new avenues of research in interaction ecology and molecular biology can be explored in the context of climate change, once monitoring data is comprehensive enough. We will also be able to provide quantification of phylogenetic signals in species extinction risk over time and to identify tropical insect lineages pre-disposed to local extinction. New sequencing technologies also allow the identification of periods of loss of genetic diversity and reductions in effective population sizes. Metabarcoding is very promising for the elimination of some taxonomic barriers for tropical taxa of functional importance, allowing biological monitoring at low cost. Scientists are also exploring the use of machine learning and citizen science to potentially identify species from pinned or live specimens captured from monitoring projects. Finally we, the scientists, should empower insect research and teaching in tropical regions, which support the majority of terrestrial diversity. This can be done by reinforcing local capacity building in tropical locations where scientists are setting up projects, something that should be included in grant applications and perhaps included in legislation in these partner countries.

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