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2 Tropical Terrestrial Invertebrates – Where to From Here?

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11 ABSTRACT

12 THERE are over one million described invertebrate species on Earth, the majority of which are
13 likely to inhabit the highly biodiverse rain forests around the equator. These are some of the most
14 vulnerable ecosystems on Earth due to the pressures of deforestation and climate change with
15 many of their inhabitants at risk of extinction. Invertebrates play a major role in ecosystem
16 functioning from decomposition and nutrient cycling to herbivory and pollination; however,
17 while our understanding of these roles is improving, we are far from being able to predict the
18 consequences of further deforestation, climate change, and biodiversity loss due to the lack of
19 comparative data and the high proportion of species which remain to be discovered. As we move
20 into an era of increased pressure on old growth habitats and biodiversity it is imperative that we
21 understand how changes to invertebrate communities, and the extinction of species, affect
22 ecosystems. Innovative and comprehensive methods that approach these issues are needed. Here
23 we discuss priorities, including conservation and sustainability, technology and methods, and
24 biogeography and ecosystem functioning for invertebrate research and highlight priorities for
25 future invertebrate research.

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27 Keywords: biogeography, conservation, ecosystem functioning, genome sequencing,
28 invertebrates, modelling, sustainability

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TEXT

If all mankind were to disappear, the world would regenerate back to the rich state of equilibrium that existed ten thousand years ago. If insects were to vanish, the environment would collapse into chaos.

E. O. Wilson, The Diversity of Life (1992)

THERE are currently 1,359,129 described invertebrate species on Earth (IUCN 2019), although, the estimated number of total terrestrial invertebrate species is thought to be closer to seven million (Stork 2018). A large proportion of these invertebrates are likely to inhabit the highly biodiverse rain forests around the equator, although the concrete evidence for this is surprisingly sparse. Due to extensive deforestation, forest fragmentation and the threat of increased drought and fire due to climate change these are some of the most vulnerable ecosystems on Earth, with many of their inhabitants at risk of extinction. However, the latest figures from the IUCN suggest that a mere 1.6% of all described invertebrate species have been assessed for the IUCN Red List compared with 68.9% of the vertebrates (IUCN 2019). Invertebrates are indisputably a particularly understudied group, probably due to a combination of the vast number of species, their small size and the cryptic nature of many taxa, and the likelihood of a high frequency of local endemics. Technological advances are, however, expected to accelerate the rate at which species are described as processes such as genome sequencing and DNA barcoding become more readily available (Lewin *et al.* 2018).

We know that invertebrates play a major role in ecosystem functioning from decomposition and nutrient cycling to herbivory and pollination. However, while our understanding of these roles is improving, we are far from being able to predict the consequences of further deforestation, climate change, and biodiversity loss, partly due to the lack of

comparative data and partly because of the high proportion of species which remain to be discovered. In addition, the role of invertebrates in ecosystem functioning in similar habitats may vary among continents due to evolutionary history. Hence, the effects of habitat loss and climate change may not be consistent across the globe.

As we move into an era of increased pressure on old growth habitats, as well as on biodiversity, it is imperative that we understand how changes to invertebrate communities, and the extinction of species, affect ecosystems. Innovative and comprehensive methods that approach these issues are needed. Here we discuss priorities, including conservation and sustainability, technology and methods, and biogeography and ecosystem functioning for invertebrate research and highlight why they are important.

CONSERVATION AND SUSTAINABILITY

While invertebrates face a multitude of pressures in tropical regions, the main threats to their existence are habitat loss and modification (Young *et al.* 2016). It is well documented that undisturbed habitats harbour high biodiversity due to the large range of microhabitats (Gibson *et al.* 2011) and play an important role in providing a species pool for surrounding more degraded areas (Bourguignon *et al.* 2017). While projects such as “Half Earth” (Wilson 2019) strive for half the planet to be protected, others suggest a re-think of economic growth (Büsche *et al.* 2017) as long-term solutions to conserve biodiversity. These are big ideas with long-term trajectories of fundamental change in the way in which we share our planet with the natural world. While these ideas are to be encouraged, *realpolitik* suggests that the uptake of these revolutionary ideas is unlikely in the short-term and that we need to think, urgently, about short-term solutions for taxa that are at risk today.

Although old growth forests should be prioritised due to their unmatched ability to support high levels of biodiversity, modified and degraded land should not be forgotten as they too provide suitable habitats for many species (Torppa *et al.* 2019, this issue). This is particularly relevant in areas where the proportion of primary habitats are diminished and where secondary or regenerating habitats provide refuge for many invertebrate species (Ewers *et al.* 2011). Conservation mapping is particularly relevant in this instance as it is a tool that, with good distribution data, can provide information about the importance of current protected areas as well as identifying areas where protection should be considered. This tool is more commonly associated with vertebrates, however, mapping invertebrate distributions would promote their conservation and highlight locations that may not have been considered for protection (Scriven *et al.* 2019, this issue).

One of the major contributors to deforestation and habitat modification is the demand for products that drives agricultural intensity and expansion (Defries *et al.* 2010). While organic farming and agroforestry have been shown to provide lower yields than intense farming practises (Poudel *et al.* 2002), better understanding of the role of sustainable agriculture as corridors or refuges for biodiversity is needed. In addition, while sustainable practices have established benefits for biodiversity and soil conditions, local management regimes and habitat regeneration have been shown to play a key role in local ecosystem functioning (Dahlsjö *et al.* 2019, Stone *et al.* 2019, this issue). For instance, increased microhabitat complexity, particularly in monocultures, has been shown to promote invertebrate species dynamics (Luke *et al.* 2019, this issue).

TECHNOLOGY AND METHODS

Invertebrates are speciose and small with relatively cryptic lifestyles that are often difficult to study. Innovative methods that enable new understanding of invertebrate behaviour and interactions, such as drivers of nesting behaviour in ants (Mottl *et al.* 2019, this issue), are key contributors to generating original and detailed data. These data are particularly valuable for ecological modelling which, led by agent based modelling, has become a prominent tool for ecological studies in recent years (Mclane *et al.* 2011). However, modelling is only as good as the available data, and so studies that describe species community dynamics are always of great importance in providing a baseline for experimental studies. This is particularly relevant for little known invertebrates such as centipedes (Phillips *et al.* 2019, this issue) and leeches (Drinkwater *et al.* 2019, this study) as well as invertebrates that contribute to ecosystem services, such as fly or beetle pollinators (Kian & Yeng 2019, this issue). Further, as the understanding of the impact of small-scale environmental barriers, such as topography, on invertebrate distribution is improving, the heterogeneity of study areas should be considered. This is particularly relevant as the composition of assemblages of flying species, such as moths, has been shown to vary with local topography (Rabl *et al.* 2019, this issue). Sampling design is also relevant when studying species interactions and functions where, for example, the trapping technique and dung type have been shown to affect the taxonomic and functional diversity of dung beetles (Raine *et al.* 2019, this study).

As technology such as genome sequencing and DNA metabarcoding is increasingly used, and the race to sequence the genomes of a large range of species is underway, our understanding of invertebrate diversity and dynamics will increase exponentially. With the emergence of species genome libraries, sequencing will become cheaper and environmental DNA increasingly available. These methods will enable understanding of the building blocks of life and

fundamental genetic changes in invertebrates as a consequence of habitat change or resource availability. While these are exciting future prospects, DNA metabarcoding is increasingly providing important data on invertebrate diet dynamics in areas of varying disturbance (Hardwick *et al.* 2019, this issue). Detailed data that shed light on behavioural changes as a response to habitat modification are vital for further understanding of ecosystem processes and dynamics.

While advances in genetic methods and statistical modelling are providing new and better understanding of ecological and environmental scenarios, advances in *in situ* experiments have enabled invaluable understanding of ecological processes. Large scale sophisticated experiments are time-consuming and expensive, but they do provide an insight into how ecosystems respond to change compared with experiments conducted in artificial environments. As the pressure on invertebrate populations increases, comprehensive species data and experiments that provide insights into the effects of environmental change are needed. Exclusion experiments are particularly effective for disentangling and quantifying the role of invertebrates in ecosystem functioning (Ashton *et al.* 2019). Being able to identify the complexity of threatened ecosystems, and predict and quantify the consequences of invertebrate demise, will play a key role in protecting them.

BIOGEOGRAPHY AND ECOSYSTEM FUNCTIONING

The functioning of ecosystems is dependent on the presence of invertebrates, yet we know relatively little about their contribution to ecosystem processes and services. Soil fauna are particularly understudied considering their importance for soil health and productivity which we rely on for food production (Cameron *et al.* 2019). In the tropics, termites and ants have been found to increase crop yield by 36% (Evans *et al.* 2011) while termites have been shown to

increase soil moisture and seedling survival during drought (Ashton *et al.* 2019). Recently there has been a focus on the contribution of invertebrates in trophic cascades where ants have been shown to play a major role in top-down control of herbivores and predators (Goldman *et al.* 2019, this issue).

While lowland tropical forests have received a lot of attention, probably due to their high biodiversity and accessibility, the niche-sets that different elevations provide support phylogenetic differences in invertebrates (Chatelain *et al.* 2019, this issue) as well as affecting functional interactions (*e.g.* pollinator-parasite) (Souto-Vilarós *et al.* 2019, this issue) and herbivory (Sam *et al.* 2019, this issue). The environmental limits associated with higher elevations (biotic and abiotic) have also produced many endemic species. These environmental barriers are likely to shift as climate change contributes to increasing temperatures with major impacts on species distributions. Climate change is also expected to increase the frequency of droughts and fires which have been shown to have a major effect on invertebrate communities such as dung beetles (França *et al.* 2019, this issue). Dung beetles play a major role in ecosystem functioning and their sensitivity to environmental extremes suggests that climate change will have a major effect on the dynamics of tropical habitats. Research into the effects of climate change on invertebrate functional diversity is therefore much needed. Elevation gradients have long been used to study climate change and may also be employed to examine the evolution and adaptability of invertebrate species and their interactions.

Whether it is food production, resilience against climate change, or trophic cascades, these studies suggest that invertebrates are key contributors to any thriving ecosystem. However, unless comparable data are gathered across the tropics, these studies will remain isolated examples. Invertebrates in communities are taxonomically and functionally different across

biogeographic regions which means that their responses to habitat deforestation and modifications also differ on different continents (Dahlsjö *et al.* 2014). Global comparative data are essential if we are to gauge fully the roles of invertebrates in ecosystems and their likely responses to habitat change or sustainable management practices. We can never ignore biogeography.

CONCLUSION

Invertebrates have been accorded relatively little attention considering their speciose nature and importance for ecosystem functioning. We have an inkling of the global importance of invertebrates but have merely scratched the surface of their complex evolutionary history, ecological roles, interactions and behaviour. As such, it is difficult to predict likely changes in the contribution of invertebrates to ecosystem functioning, such as nutrient cycling, pollination and herbivory. Such predictions are vital in order to prevent large scale decline of invertebrate populations with severe consequences for ecosystems and the services they provide to those dependent upon them. Better understanding of invertebrate ecology, behaviour and interactions is therefore of high importance. Comprehensive and comparable data provide the foundation of any good explanatory model or hypothesis and the collection of such data should remain a high priority. Innovative methods that tease apart drivers of behaviour or functions should also be pursued including large scale *in situ* experiments which enable habitat level examinations of ecosystem processes. The likely catastrophic consequences of invertebrate demise demand such research be given a high priority.

188 DATA AVAILABILITY STATEMENT

189 No unpublished data were used to produce this paper.

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