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Authors

Beck, Jan
McCain, Christy M.

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Just bird food? – On the value of invertebrate macroecology

Jan Beck¹  and Christy M. McCain^{1,2} 

¹University of Colorado, Museum of Natural History, 265 UCB, Boulder, CO 80309, USA. jan.beck@colorado.edu;

²University of Colorado, Department of Ecology and Evolutionary Biology, 265 UCB, Boulder, CO 80309, USA. christy.mccain@colorado.edu

Abstract:

Recent reviews have highlighted the dominance of vertebrates and plants in macroecological and biogeographical publications while invertebrates are underrepresented despite their global ecological relevance and vast diversity. We argue that although the study of invertebrate biogeography and macroecology has data limitations and thus lags behind in global research coverage, it has left a strong mark on the development of the discipline and has continuing potential to significantly shape its future. First, we detail how historical collecting and identification impediments caused decelerated progress at the macro-scale. Second, we show the quantitative impact of early invertebrate studies in contrast to lowered current representation. Third, we discuss ways in which authors, editors, and reviewers may foster invertebrate studies in macroecology. These include an honest appreciation of the value of study replication, of understudied but diverse taxa, and of the ecological traits that make invertebrates unique in comparison to vertebrates (e.g., wider array of life cycles, symbioses, and ecological niches), as well as the expanded potential for experimentation and manipulation.

Highlights

- In early large-scale ecological research, invertebrate studies were both plentiful and highly influential based on quantitative literature surveys, but they are under-represented in recent macroecological literature.
- Reasons for under-representation include gaps in knowledge on systematics, distributions, traits, and the challenges involved in filling them.
- We argue that invertebrate studies are vital: they provide the bulk of global biodiversity, permit study replication, allow detection of commonalities and contrasts in patterns and mechanisms across taxonomic groups, provide model systems in functional ecology, and are often suitable for field experimentation.
- We aim to encourage invertebrate researchers to continue collecting high-quality data and producing strong analyses, to equip them with arguments for funding and publishing, to foster appreciation for the value of invertebrate studies among biogeographers, macroecologists, and editors; and to spark fruitful discussions with the ornithologist from the lab next door.

Keywords: Biodiversity, Data limitation, Insects, Invertebrate macroecology, Literature survey, Research novelty, Study replication

Titley et al. (2017) and Beck et al. (2012) highlighted the heavy bias of macroecological publications towards vertebrates and plants (see also Hortal et al., 2015). Invertebrate macroecology faces particular challenges (detailed below) that may explain this underrepresentation. These challenges relate to two issues that must not be conflated. First and trivially, difficulties in attaining high-quality data can lead to studies based on poor data, such as extremely low sample sizes, which may be used as an excuse for inferior scientific rigor. We hold to the opinion that only high-quality data can lead to valuable insights. Second and much harder to judge, the time-delay in attaining high-quality data may diminish the novelty of insights (e.g., because vertebrate ecologists have

uncovered them years ago). We acknowledge that an open discussion is warranted on how valuable a study with the main selling-point “this is the first study on this topic in taxon XY” really is.

Robert MacArthur pointed out that foundational ecological mechanisms should not be taxon-specific. Once general mechanisms are uncovered reliably on a sufficiently inclusive taxonomic group, re-studying them on other taxa would be “not only a little masochistic... it also misses the point. We are looking for general patterns that we can hope to explain” (MacArthur, 1972 [1984], p. 176). Macroecology is devoted to these generalities of patterns and mechanisms across time and space, which raises the question whether invertebrate macroecology is not a highly

“masochistic” endeavour that entirely “misses the point”? Contrary to this view, research of “general” ecological patterns and mechanisms can hardly be general if it systematically excludes a large majority of taxonomic lineages from study.

Here we want to critically discuss the value of invertebrate macroecology or, more broadly, ecological biogeography, hoping to spark a deeper discourse on how to make better use of invertebrates for understanding large-scale ecology (Fig. 1). If invertebrate studies are deemed valuable, we may want to change attitudes and approaches that currently lead to its perception as second-class science. If macroecology deems invertebrate research of little value, we should be transparent and forthright to save the invertebrate researchers the effort. Many of our arguments do equally apply to conservation research, where (particularly at large geographical scales) invertebrate research is underrepresenting the actual degree of invertebrate extinctions and population declines, as well as their functional relevance for ecosystems.

Part I: The challenges and rewards of being an invertebrate macroecologist

Undersampling and taxonomic uncertainties are not problems confined to invertebrate studies, but they play prominent roles in contrast to vertebrate or plant studies (Coddington et al., 2009; Hortal et al., 2015). The reasons are manifold and partly historical. Invertebrates are often small and hard to distinguish (often needing microscopic dissection of sexual organs), many species are of no particular aesthetic appeal to the public (Troudet et al. 2017), and many are of no direct, known economic importance (despite the existence of some agricultural pests with huge economic impact). Consequently, many more researchers have collected and compiled knowledge on plants and vertebrates, often in the context of hunting and agriculture at initial stages. In comparison, the taxonomic study of obscure invertebrates was left to a few enthusiasts or pest managers (a continuing trend; Hopkins and Freckleton, 2002). Much more background knowledge on systematics, distributions, and traits has accumulated for vertebrates and plants, and this created a positive feedback process. Downstream investigations of phylogeny, geographic ranges, and biodiversity focused on these well-described groups, making them even more fruitful for further study. Contrary to this uneven research effort, the much higher species richness of invertebrates (Stork et al., 2015) would require more, not less effort of data collection, processing, and identification (Diniz-Filho et al., 2010; Cardoso et al., 2011; Basset and Lamarre, 2019).

To work on large-scale invertebrate ecology, one often has to collect or mobilize new data (in the field or in museums), identify species (possibly including taxonomic revisions), and sort out a reticulate nomenclature. This reduces the time for reading literature, performing analyses, and writing papers. It also requires unique skills, for example microscopic insect morphology, necessitating a substantial time investment at the cost of diving deeper into ecological theory, data analysis, or other skills required for top-notch science. Some of those steps can be shortcut when

working on vertebrates or plants as relevant data are already available (e.g., online: IUCN, 2010; Boyle et al., 2013). It is hard to compete with scientists who can substantially fast-forward a project by skipping the data collection aspects of macroecology.

There may be yet another layer of feedback due to the perception of invertebrate studies as *a priori* less interesting or well-supported. Repeatedly, in our experience, authors are asked by reviewers to justify why a given topic was studied in insects, implying in the context, why not in a “normal” taxon? Reception is often not encouraging. For example, Erwin’s (1982) estimate of up to 30 million arthropod species (cf. Stork et al., 2015) could be considered a highlight of biodiversity science at the time, but the paper only received a modest 1300 citations, and the impact factor (IF) of the journal is less than 0.5. For someone aiming at a professional career in macroecology it may not pay to go through all this effort when it is not rewarded in terms of paper acceptance, journal impact, or citations (Krell, 2002). Notably, there is a perception that the general public perceives vertebrate news and scientific research, particularly for birds and mammals, as much more engaging than non-vertebrates (cf. Fig. 2). Perhaps



Figure 1. White wagtail (*Motacilla alba*) with a load of invertebrate bird food (picture by Wolfgang Forstmeier).



Figure 2. While violin beetles (*Mormolyce* sp.; pictured specimen from Sabah, Malaysia; picture by Jan Beck) thrill some beetle specialists and collectors, there is little knowledge about, or interest in them in the general public, as indicated, for example, by the Wikipedia¹ one-liner for the genus).

¹ https://en.wikipedia.org/wiki/Violin_beetle, accessed May 2020

this bias exists because we eat them and they ate us, not to mention their use in pre-industrial agriculture and transportation or as pets. But science should not be as subjectively biased. In fact, if we do not understand biogeographic patterns in the vast majority of animals (~95% are invertebrates) or multicellular organisms (~70% are invertebrates; IUCN 2020), do we have a handle on macroecology at all?

Part II: Have invertebrate studies led to any major progress in macroecology?

For a quantitative assessment of the contribution of invertebrates to macroecology, we turned to the *Foundations of Macroecology* collection of 46 papers by Smith et al. (2014) and extracted details on the studied taxa. Furthermore, more subjectively, we extracted data on study taxa from the 55 early or seminal “key citations” for 26 “patterns of principal concern” in *Patterns and Process in Macroecology* (Gaston and Blackburn 2000; as listed in their Table 1.1). Invertebrate datasets were similarly represented as vertebrates and plants in these foundational macroecology studies (Fig. 3). Invertebrates had a significantly higher impact than what might be expected when judged based on recent total publication output (Beck et al., 2012, Titley et al., 2017). As a reminder of some highlights of the past, species-abundance relationships became a topic of research based on tropical butterfly collections (Fisher et al., 1943), while Morse et al. (1988) used tropical beetle data to add body size as a third, related variable. Marine bivalves were used to shed light on the nature of mass extinctions (Jablonski, 1986). MacArthur & Wilson (1967 [2001]) relied on ant data, among others, to elucidate their ideas on island biogeography, and many follow-up studies on the topic were also carried out on invertebrates (e.g., Simberloff, 1976, Brown & Kodric-Brown, 1977). It is

impossible to know, of course, which of the current publications will be judged important in 50 years.

Part III: Making better use of invertebrates in macroecology

Novelty is good, replication is better

The extraordinary emphasis on “novelty” in the current publishing landscape encourages research practices that lead to greatly inflated statistical error (Parker et al., 2016, Forstmeier et al., 2017), which has been linked to “why most published research findings are false” (Ioannidis, 2005). Among such critical practices are tests of hypotheses that were formulated (or specified) only after data were known (*post-hoc*), and various attempts to mine for statistical significance by trying different analytical protocols (e.g., data filtering, modifying model specifications; *p*-hacking). Publication bias towards desired results, and an underreporting of the analytical trial and error that led there, make some published studies appear much more rigorous than they really were. Forstmeier et al. (2017) advocate strong scepticism against spectacular results in empirical disciplines as (unconscious) confirmations bias of researchers is not countered, but fostered, by the current constraints of publishing and career-advancement.

In a largely non-experimental discipline such as biogeography, the only difference to the disciplines treated by Parker et al. (2016) and Forstmeier et al. (2017) is that the detection of non-replicability, and hence ultimately proof for findings being false is more challenging. Thus, we may expect in our discipline, too, that many high-impact studies from the top journals will eventually turn out to be statistical false-positives. Replicating studies with new data is crucial to uncover these, but this is not straightforward in a discipline of global, non-experimental studies that already tends to

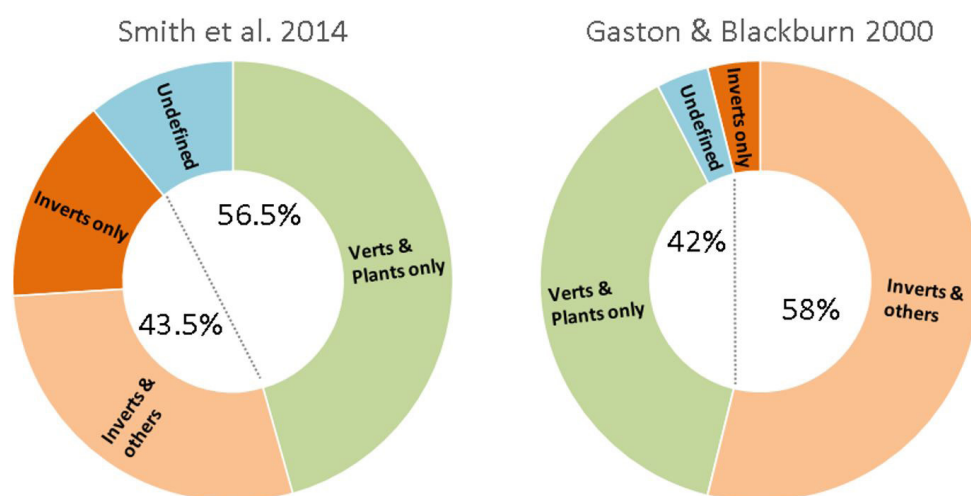


Figure 3. Study taxa in all papers of Smith et al. (2014, left) and in the key citations supporting 26 patterns of principal concern in Gaston & Blackburn (2000, right). Dashed lines and percentages distinguish studies with and without invertebrates. Data are available upon request.

use all available data on a given taxon in each study. The obvious way to test a general, taxon-independent (macro)ecological hypothesis is to re-study it in another taxon.

Invertebrate biogeographers and macroecologists, due to data limitation (part I) often find themselves working on topics that had been treated years or decades earlier in plants or vertebrates. What is currently considered a disadvantage (i.e., not being the first to publish) should be viewed as an asset. A topic is not settled when a novel pattern or mechanism has been first published, but only if it still stands after manifold attempts to falsify it (Popper, 1934 [2002]). If results found for vertebrates or plants cannot be replicated with invertebrate data, they clearly lack the claimed generality. And the primary endeavour of uncovering critical mechanisms may indeed involve the differential presentation and biology among taxonomic groups and not only those aspects shared among them. For example, Grünig et al. (2017) used sphingid moths to test the idea that climate change velocity since the Pleistocene affected species range size distributions (proposed earlier based on vertebrate data). By rejecting the hypothesis with their data, they showed that it cannot be a general mechanism that explain patterns in all (or most) taxa while inviting new, refined hypotheses (such as different relevant time windows for different taxa) to be tested in future studies. Similarly, Grenyer et al. (2008) reported that some global geographic patterns are not even predictive among vertebrate groups. Hence, it appears even less likely that they would match among birds and beetles, for example.

For authors, this means that there is scientific value in aiming at rejection, not confirmation, of a previously published hypothesis (with adequate data and methods). Contrary to this, researchers tend to be disappointed if their data do not match the investigated hypothesis, and it has been suggested that they might even twist data and methods until it does (Simmons et al., 2011). Even worse, reviewers and editors may push them into that direction. The first author experienced this repeatedly in the top journals of our discipline. We think this is partly a structural issue. It is an understandable practice to send manuscripts for review to those who published on a topic previously, as they are obviously specialists. However, they are also usually the ones whose results are challenged by critical tests. Authors often have to deal with reviewers' *post-hoc* hypotheses aimed at explaining why a test of a general pattern turned out differently than that of the original publication. However, if all players (authors, reviewers, editors) have a negative tendency towards challenging published knowledge with new data, we can only expect confirmatory publications of little merit for the progress of science. Editors should actively appreciate the value of replication and hypothesis rejection in their decisions (Currie, 2015; Currie et al. 2020). As long as "not having found something" is perceived as either lack of novelty or as an error (because *Science* paper XY showed the effect), we miss a crucial part of the scientific method.

Theorize, seek taxonomically diverse data, and value data providers

Looking through the past studies deemed important in macroecology (part II), some common features of these papers became obvious. Typically, a theoretical idea was first explored logically and mathematically, and then many available datasets from various sources were used to illustrate or test it. Studies appeared driven by theory, not by the taxon and dataset at hand. As a tell-tale sign, titles and abstracts often did not even mention the studied taxa. It was the multitude of datasets supporting a pattern that provided credibility. Thus, it may benefit researchers building new large-scale ecological theory to illustrate a pattern not just with easily obtainable datasets (usually vertebrates or plants), but to maximize the taxonomic diversity of the datasets.

However, if individual researchers spend their professional time providing high-quality datasets, they must get career-building credit. As a positive development, some journals such as *Global Ecology and Biogeography* now allow source data citations outside the usual citation limits. Data papers, as published now, for example, in *Ecology*, are also helping to give visibility and credit to data providers. In the days of *Google Scholar* or other online citation tools, high citation numbers for a dataset lead to recognition no matter where they were published. Inviting data contributors to co-author papers may help motivate the continuing provisioning of high-value data on understudied taxa toward a broader biogeographical or macroecological synthesis. For example, Colwell et al. (2016) presented a novel approach to integrate the mid-domain effect with taxon-specific environmental drivers to explain elevational diversity patterns (developed by the first two authors of the paper). They illustrated and tested the approach on a wide variety of elevational datasets including many on invertebrates, listing all data-contributors as co-authors.

Maps are nice-to-haves, but samples of adequate quality and sufficient size are must-haves

Maps are great for data visualization and have been heavily advocated as a macroecology research tool (Ruggiero and Hawkins, 2006). However, they are unnecessary for statistical inference, pattern description, and hypothesis testing. A few hundred good data points are usually more than sufficient to detect a relevant pattern, so there is no need to obsessively strive for, or demand, high-resolution maps of 10,000 or more pixels. Thus, if there is sufficient data for a map, show it. But when working on a data-limited taxon, aiming for solid data points may be more valuable than colourful maps. Similarly to MacArthur's (1972) requirement of a "sufficiently inclusive" study taxon (i.e., not being too specific due to its evolutionary history), it is important to choose sufficiently inclusive study regions (i.e., aiming for geographical replication by confirming a relationship in various parts of the world). For example, Beck et al. (2017) used a compilation of globally spread, local field studies of geometrid moths

to analyse elevational richness gradients and their hypothesized environmental drivers. Attempts to map the richness of this extremely diverse group, however, would have been futile and probably misleading at the current state of knowledge, as the geographic spread of many rare species is insufficiently (or not at all) known yet.

Invertebrates are suitable for large-scale experiments

Experiments are useful and often indispensable to elucidate ecological mechanisms, but ecosystem-wide experiments beyond primary producers are limited by feasibility, scale, and legal constraints. While microcosms have been used for community studies (Benincà *et al.*, 2008), we are just at the beginning of replicated experiments at spatial scales relevant for macroecology (Faile *et al.*, 2015). Invertebrates are typically smaller and more abundant than vertebrates, which make them more feasible for experimentation. Furthermore, there are fewer legal obligations (e.g., permitting, Animal Care and Use Committee protocols) for experimenting with invertebrates.

The last shall be first: Embrace new technologies

Having a late start can sometimes be a primer for adapting new technology faster than those who seem to have no need for it. Taxonomy and taxonomic inventories in understudied groups profit from DNA-aided approaches (e.g., BINs, Ratnasingham and Hebert, 2013; meta-barcoding, Cristescu, 2014; for applications see also deWaard *et al.*, 2019, Karlsson *et al.*, 2020). While resistance to such approaches is fostered by publications pointing out manifold options for error, classical taxonomy also undergoes constant revisions (which is another way of saying: it has been wrong). Analogously, poor field data may more easily foster a mind-set of embracing a probabilistic view on species distributions (i.e., via distribution modelling), which has been judged by some a more reliable assessment than seemingly solid observations (Jetz *et al.*, 2019). Embracing such approaches may offer relevant assistance to close the data gap faced by invertebrate macroecologists. Furthermore, such approaches can be combined with collaborative online databanks and analytical workflows that would allow for continuous update and reanalysis (Jetz *et al.*, 2019).

Make use of ecological specialization and trait variability

Testing hypotheses on ecological mechanisms is supported by utilizing taxa with a wide range of traits that allow assessing generalities but also understanding and predicting exemptions to the rule. Invertebrates offer a wide variety of traits, such as modes of thermoregulation, dormancy, migration, mobility, degrees of sociality, resource specialization, symbiotic relationships, life cycles and reproductive modes that by far outranges the variability found among vertebrates. Their impact on macro-patterns are prime topics of research.

For example, specialization, in particular diet specialization among herbivores and parasitoids, is common among insects (Forister *et al.*, 2015). These intimate predator-prey relationships offer potential for developing theory and studying topics that are weakly expressed, if at all, in vertebrates. It invites, for example, studying guild-wide patterns, such as among the insects occurring on a particular plant species (e.g., Strong *et al.*, 1984; Novotny *et al.*, 2002), moving the analytical focus from geographical to resource space. Niche breadth surely impacts ecological macro-pattern, and insects will allow testing concepts and predictions over a large range of specializations. Several recent studies used the unique feeding habits of insects to investigate the more-individuals hypothesis and its inherent links among productivity, food availability, abundance, and richness along elevational gradients (Classen *et al.*, 2015, Gebert *et al.*, 2020, Mayr *et al.*, 2020).

Comparisons among thermoregulatory modes to understand the link of environment and richness have been fruitful among four vertebrate groups (Buckley *et al.*, 2012), while only the inclusion of invertebrates can provide more phylogenetically independent samples (e.g., Ballesteros-Mejia *et al.*, 2017). The huge diversity among invertebrates is generally an asset in this context, as there are more cases of convergent evolution among traits of interest.

Conclusions

The large proportion of invertebrates among the important macroecological studies of the past indicate that their impact is high, despite their underrepresentation in recent publication numbers as concluded in earlier reviews. While studying invertebrates has some undoubted challenges, it is well worth it. In a natural world embroiled in overexploitation of habitat and modified climates, it may be that as insects disappear so do all organisms. It stands to reason that the scientific community, and biogeographers in particular, should be very concerned about improving our understanding of global patterns in insects and other invertebrates.

In particular, we came to the conclusion that masochism (*sensu* MacArthur, 1972) is a good thing. Replicating, hence testing what, superficially, seems to be known already is at the essence of empirical science. Studying a general ecological pattern on another taxonomic group, particularly hyperdiverse ones, or in another region is just the right test to do. Maybe there was less need for this in MacArthur's time, for example, because there were fewer scientists with less pressure to publish the spectacular; or maybe he was just not fully aware of the problem. For those striving for novelty, focussing on topics and methods that are particularly suitable to be addressed with invertebrate data may be fruitful.

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