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Opinion

Macrobehaviour: behavioural variation across space, time, and taxa

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We explore how integrating behavioural ecology and macroecology can provide fundamental new insight into both fields, with particular relevance for understanding ecological responses to rapid environmental change. We outline the field of macrobehaviour, which aims to unite these disciplines explicitly, and highlight examples of research in this space. Macrobehaviour can be envisaged as a spectrum, where behavioural ecologists and macroecologists use new data and borrow tools and approaches from one another. At the heart of this spectrum, interdisciplinary research considers how selection in the context of large-scale factors can lead to systematic patterns in behavioural variation across space, time, and taxa, and in turn, influence macroecological patterns and processes. Macrobehaviour has the potential to enhance forecasts of future biodiversity change.

Highlights

Behaviour is often the first response of organisms to rapid environmental change and can be a key mediator of ecological responses at higher organisational levels.

Macroecology seeks to understand patterns and processes that emerge from the interaction of many smaller components, and behaviour is an important but understudied category of component.

We propose the new field of macrobehaviour, which aims to unify behavioural ecology and macroecology. Researchers from both disciplines can take advantage of new tools, approaches, concepts, and data, and ultimately ask new interdisciplinary questions.

'Bigging up' behaviour

Behaviour can be a key component of responses to rapid environmental change [1–3] and can also structure patterns above the scale of populations, from context-dependent dynamics in ecological communities [4] to range boundaries for species geographical distributions [5]. Despite these clear links, explicit consideration of behaviour as a mediator of ecological processes across large scales is broadly missing [5,6]. Accurately predicting the effects of environmental change on ecological communities will likely require bringing behaviour into the fold. We believe that research at the interface of **macroecology** (see Glossary) and **behavioural ecology** would greatly enhance both fields.

Behavioural ecology aims to elucidate how animal behaviour influences, and is shaped by, ecological and evolutionary processes [4]. Yet, how behaviour varies across large extents in space, time, and taxa (i.e., dozens of populations, generations, or species [7]) is broadly unquantified. Existing behavioural ecological theory is based almost exclusively on selection. Explaining patterns of behavioural variation above the population level requires considering factors such as dispersal limitation and biogeographic history. In other words, selection happens against the backdrop of larger-scale processes (Figure 1). For instance, extra-pair paternity in birds exhibits a latitudinal pattern [8,9], with higher rates occurring at lower latitudes. However, this is not a simple case of selection varying along a latitudinal gradient; the pattern also results from variation in biogeographic and diversification histories of different regions. Scaling up comes with the sorts of challenges macroecologists have been grappling with for decades (e.g., **transmutation**, nonlinearity, and **emergent properties**).

Macroecology seeks to explain patterns such as diversity gradients, abundance distributions, and the nature of geographic ranges across large spatial, temporal, or taxonomic extents [7]. Four correspondingly large-scale processes are traditionally invoked to explain these patterns: speciation, movement, **maintenance**, and extinction. Given that all these processes can be influenced by variation in behaviour within and across lineages, and could iteratively influence

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behaviour itself, we believe there is much to be gained by linking these two disciplines under the framework of **macrobehaviour** (Figure 1).

What is macrobehaviour?

Although rare, research that integrates behavioural ecology and macroecology exists (Figure 2; Boxes 1 and 2). Unfortunately, these works are currently scattered, hindering the potential to identify commonalities that could elucidate systematic links between behaviour and macroecology. Conceptually, we believe that there are also opportunities to push beyond existing efforts by considering explicitly how selection operates against the backdrop of macroecological processes, and by developing solutions to issues that arise when scaling up from dynamics at the individual or population level to macroscale patterns and processes. We believe that the most effective way forward is to establish a new field that coalesces current research threads and fosters a coherent research community that can recognise recurring themes, responses, and questions, and take aim at new challenges.

We define macrobehaviour as the 'investigation of variation in behaviour over large geographic, taxonomic, and temporal scales, and the ecological and evolutionary consequences of this variation', which draws on the definition of macrophysiology [10]. Macrobehaviour can be envisaged as a spectrum across which investigators from the established disciplines borrow data, methods, and concepts from one another. At one end, we can quantify variation in behaviour at large scales, and apply macroecological methods and concepts to test existing behavioural ecology theory in new ways. At the other end, we can use data and concepts from behavioural ecology to explore the influence of behaviour on macroecological patterns and processes (Figure 2; Boxes 1 and 2).

Macrobehaviour seeks to combine the mechanistic perspective of behavioural ecology with macroecology, which is classically focused on emergent properties of aggregated ecological entities (e.g., species in an assemblage; [11]). Here, we focus on the behaviour of animals, but we recognise that behaviour is observable in plants, fungi, bacteria, and protists, and the same concepts apply broadly across those groups. We arrange examples of existing work along a spectrum in Figure 2 from left to right, but the exact placement is somewhat arbitrary and simply aims to illustrate the range of possibilities under the macrobehaviour umbrella.

We note that the term macrobehaviour has been used in a handful of works in social science [12], materials science [13], and comparative psychology [14] in reference to other phenomena, but to our knowledge has not been used in biology.

Enhancing behavioural ecology by drawing on macroecology

Understanding how the behaviour of animals evolves in response to variation in the abiotic and biotic environment is the major focus of behavioural ecology. The first step towards this endeavour is often to quantify variation in the behaviour of interest across an environmental gradient that is hypothesised to drive selection. The more of the gradient that can be captured, the stronger the test will be. By encompassing a wide range of environmental conditions, such data also allow us to evaluate the extent to which a given theory is **generalisable** (e.g., across taxa or continent) versus context-dependent [15,16] (Box 1). If high context-dependency is evident, we can then use this substantial dataset to tease apart which aspects of the context are most important. These are the tools of macroecology (Figure 2, left of spectrum).

Examples of this approach include Oteyza *et al*. [17], who leveraged differences in body size and survival probability across latitude to test hypotheses about parental risk-taking. The large spatial

Glossary

Behavioural ecology: the study of behaviour in an ecological and evolutionary context.
Emergent property: property of an ecological unit that is unpredictable from observations of its components.
Generalisable: conclusions that can be applied to multiple contexts such as different locations, taxa, and times.
Macrobehaviour: the investigation of variation in behaviour over large geographic, taxonomic, and temporal scales and the ecological and evolutionary implications of this variation.
Macroecology: the study of emergent phenomena across large spatial, temporal, or taxonomic scales.
Maintenance: acquisition and allocation of energy.
Territoriality: a form of social dominance in which the resident individual or group has priority of access to resources or mates in a particular area.
Transmutation: mathematical process of scaling up changes the properties of functions and becomes increasingly problematic with increasing non-linearity and variance.

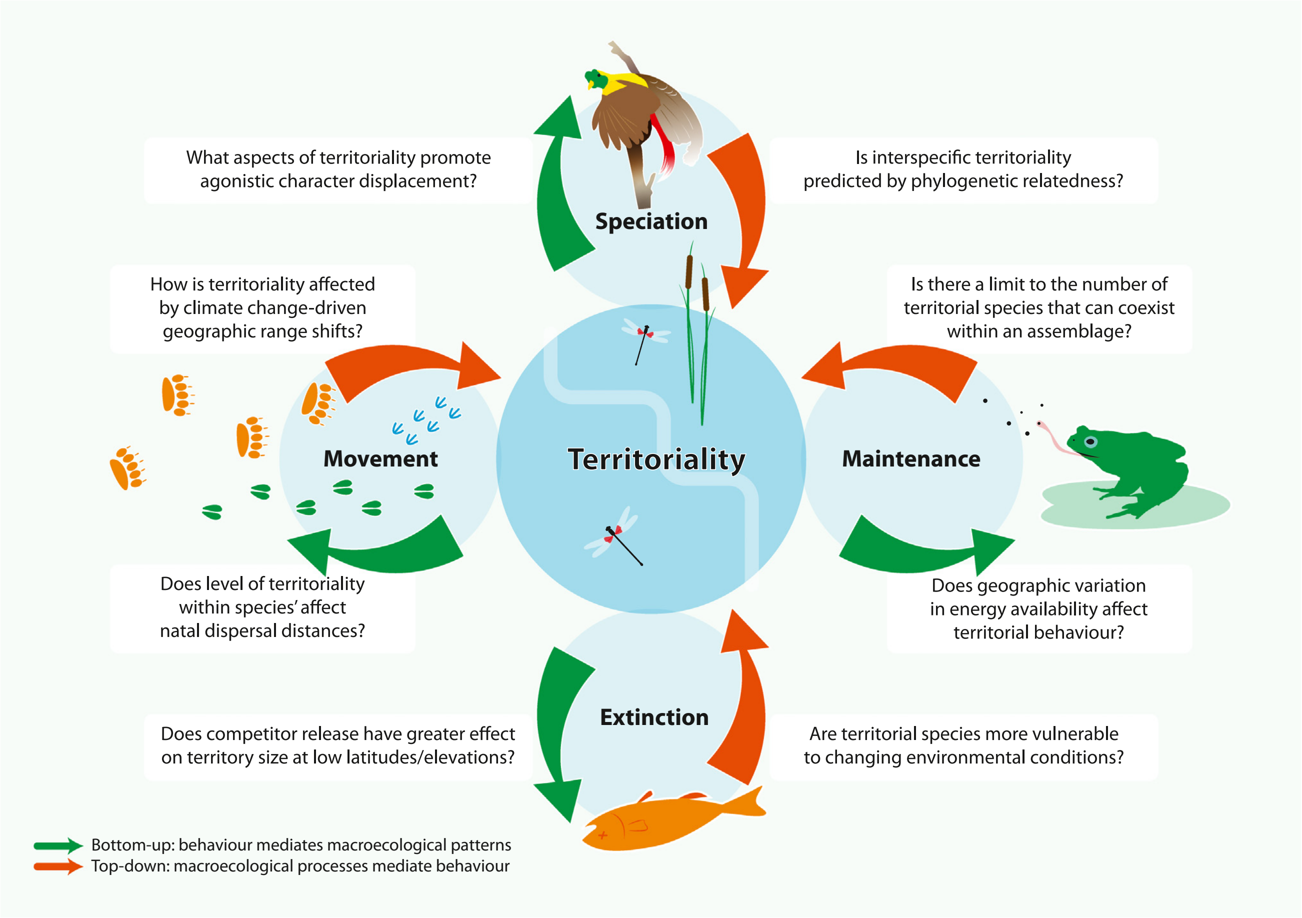

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Figure 1. New questions that are possible under the macrobehaviour framework. Here, we use territoriality as an example of a type of behaviour that can influence (bottom-up) or be influenced by macroecological processes (top-down). In some cases, these are adaptations of existing hypotheses, while others are newly proposed here. For example, the Species Interactions–Abiotic Stress Hypothesis [72] predicts that release from an interference competitor due to their extinction should have a greater effect on range boundaries at low elevations or latitudes than at high elevations or latitudes. Many of these questions also include an element linked to rapid environmental change or disturbance. Note that these questions are not exhaustive for this topic but give a flavour for the types of questions that can emerge from the macrobehaviour framework.

and taxonomic scale also enabled the broad conclusion that smaller, longer-lived birds were more risk averse [17]. Using data collected along a latitudinal gradient, Ojeda *et al*. [18] showed that the non-random orientations of nests in 25 cavity-nesting bird species were not angled to optimise solar radiation, and instead appear to be driven by a complex interplay of multiscale factors. At a global scale, the influence of climatic conditions on breeding season was predictive of reproductive strategies for harvestman (Opiliones), suggestive of broad macroecological patterns in sexual selection [19].

Considerations of scaling up

Behavioural theory has largely been developed on, and tested using, scales below that used by macroecology. Whilst this is not an issue in itself – those theories may work perfectly well at the scales for which they were intended – when we try to apply these theories at larger scales, problems could arise. We touch on this briefly here and refer the reader to [7] for a more in-depth discussion.

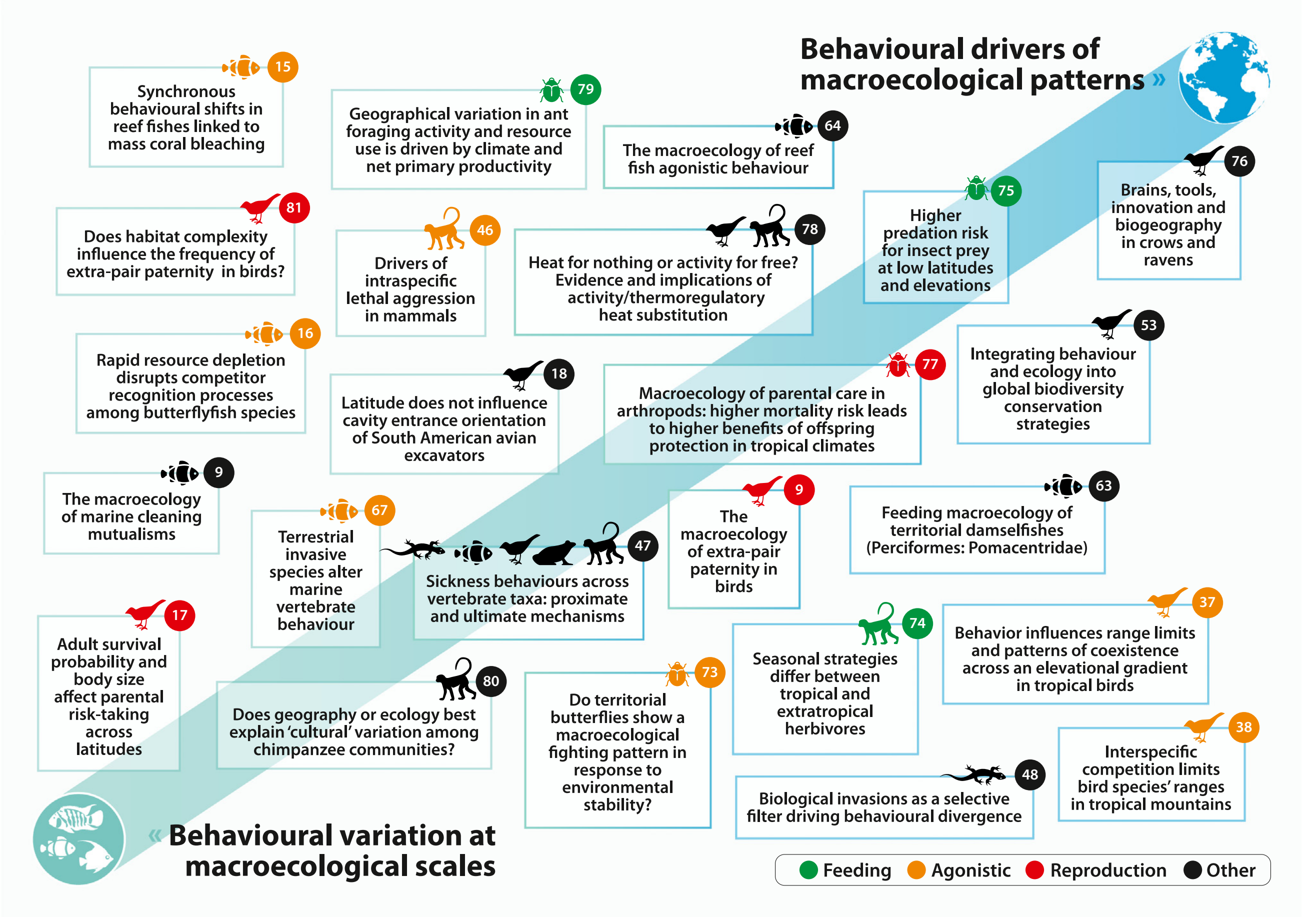

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Figure 2. The spectrum of macrobehaviour. Recent examples are represented by paper titles, animal class (bird, mammal, fish, reptile, amphibian, or insect silhouette), and type of behaviour (colour). This is not an exhaustive list of all papers that would fit under the umbrella of macrobehaviour but is intended to illustrate its broad reach across the spectrum. Papers were identified with a whole-text search for 'macroecolog*' AND 'behavio*' in Web of Science on 6 January 2023 and filtered for relevance. See [9,15–18,37,38,46–48,53,63,64,67,73–81].

One consideration is that the dominant processes may change with scale [20]. For example, if we think about how the abundance of a population changes in response to rising temperatures, behavioural responses such as behavioural thermoregulation [21] may dominate. However, if we scale up to thinking about how rising temperatures affect aggregate patterns, such as abundance distributions of species assemblages, larger-scale processes such as colonisation and extinction may dominate [22]. That is not to say that behavioural thermoregulation of different populations is not important but that it can only inform predictions about abundance distributions if it is embedded within the context of larger-scale processes.

Abundance distributions are emergent because their characteristics (e.g., evenness, and frequency of rare/common species) cannot be predicted solely by understanding an individual component (abundance of one species) of the system. Emergent properties do not directly scale or relate to the properties studied at smaller scales [7] but are often used in place of smaller-scale mechanistic properties to enable broad general patterns to be identified. For a more direct example that would fall under macrobehaviour, the distribution of foraging strategies across a species assemblage cannot be predicted from the foraging strategy of one species, and

Box 1. Reef fish across the spectrum

Coral reefs are globally important hyperdiverse ecosystems that offer an excellent opportunity to explore macrobehaviour. Distributed throughout the tropics, they show clear geographical patterns in species diversity [40] facilitating replication across locations, and species interactions abound leading to rich behavioural tapestries [61].

Meta-analyses that combine data from existing literature are one way to tackle macrobehavioural questions. Data from 231 species across eight sites in the Atlantic and Pacific Oceans, and the Mediterranean Sea revealed that relationships between cleaner fish and their clients were structured by neutrality, offering fundamental insights into species coexistence and community assembly mechanisms [62]. Analyses of bite rates for damselfishes from three ocean basins across a gradient of 8°C variation in mean annual sea surface temperature (SST) suggested that higher metabolic requirements in warmer water drove higher feeding rates in aggressive farming damselfishes [63].

Macrobehaviour of coral reef fish has also been explored with primary data. Fontoura *et al*. [64] quantified change in reef fish agonistic interactions across a 34 000 km longitudinal gradient of species richness. Agonistic networks were nested in structure with a core of highly aggressive territorial species, and similar frequencies of agonistic interactions regardless of regional richness. Therefore, emergent agonistic behaviour appears to be constrained locally, supporting the idea that common structuring mechanisms underlie species coexistence [64].

Coral reefs are experiencing increasingly frequent and severe disturbances [65]. A global coral bleaching event in 2016 led to mass mortality of corals across the Indo-Pacific, providing a natural experiment to explore effects of rapid resource depletion, replicated across multiple regions (Figure I). Coral-feeding butterflyfishes became less aggressive, as predicted by economic defendability theory [15], and their ability to recognise, and respond appropriately to, competitors was compromised [16]. The replication of this response across multiple regions offers strong support for its generalisability. Longer-term disturbances also offer useful experimental set-ups. A subset of Chagos Archipelago islands were invaded by rats in the 1800s, disrupting nutrient flows that connect terrestrial and marine systems via bird guano [66]. This disruption depleted the nutritional quality of damselfish food around rat-infested islands, causing their territorial behaviour to lessen, with unknown consequences for the ecosystem [67]. By exploiting environmental disturbances, we can both test fundamental behavioural theory and reveal behavioural adjustments that could have important ramifications for vulnerability of coral reef communities due to disruption of species coexistence mechanisms and ecosystem function.

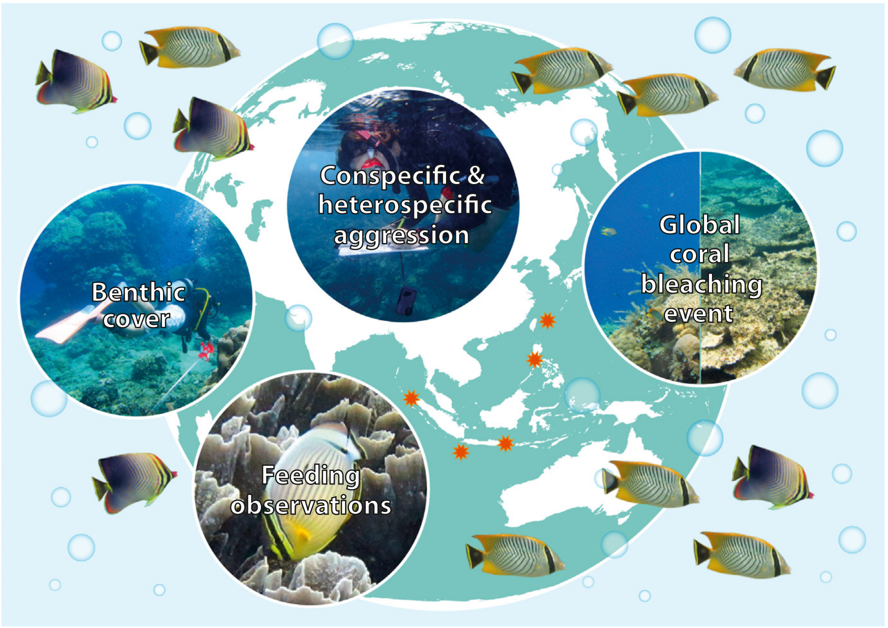

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Figure I. Example set-up for reef fish macrobehaviour research. Individuals from 38 species of butterflyfish were observed at 17 reefs across five regions (stars on map) in the central Indo–Pacific, spanning ~4000 km latitudinally and ~3000 km longitudinally. Data on aggression, feeding, and benthic (coral, algal, or substrate) cover were collected before and after a global coral bleaching event in 2016 that caused mass coral mortality, providing a natural experiment replicated across multiple localities. Photo credits: Erika Woolsey, Sally Keith.

we would need to consider other factors such as habitat structure and interactions between species (already the purview of behavioural ecology) against the backdrop of assemblage composition generated by speciation, dispersal, and extinction (macroecology).

Finding a way to predict emergent properties mathematically by linking equations of individual or population level behaviour, to equations at larger hierarchical scales, is further hampered by the transmutation problem [23], which states that scaling of equations across hierarchies can be exact only in systems with linear responses or no variability – a rarity in ecological systems. The use of probability distributions as dependent variables (e.g., Bayesian approaches) and process-based or mechanistic models can offer solutions [20,24]. However, a significant challenge remains, both for modelling and to target primary data collection, in identifying which small-scale mechanisms are essential for predicting macroscale patterns, while remaining tractable and interpretable [22].

Harnessing environmental change as natural experiments

Identification of the behavioural impacts of anthropogenic global change is one factor that motivates many papers outlined in Figure 2, and therefore global change is at the heart of the macrobehavioural endeavour. However, in addition to providing the impetus for examining geographical variation in behaviour, environmental changes can offer natural experiments (Box 1). Urbanisation is a prime example. Associated with sweeping changes in abiotic and biotic conditions, an entire subfield of behavioural ecology aims to understand the mechanisms driving urban shifts in behaviour [25]. For instance, the combination of increased noise with decreased predation and pathogen pressures in urban environments selected for increased call complexity in urban Túngara frogs (*Physalaemus pustulosus*) in comparison to their forest-dwelling counterparts [26], and asymmetries in bird dominance interactions were more likely to lead to aggressive exclusion in highly urbanised environments [27].

Invasion biology examines the impacts of non-native species after anthropogenic factors lead to their establishment in a new location [28]. A growing number of empirical case studies demonstrate that behavioural interference often plays a key role in determining the pace and outcome of invasions [29]. In both the USA and China, the introduction of the mosquito *Aedes albopictus* has driven a rapid decline in *Aedes aegypti* owing to an asymmetry in the fitness impacts of reproductive interference [30,31]. Similarly, agonistic interactions between a native gecko species (*Lepidodactylus lugubris*) and the invasive house gecko (*Hemidactylus frenatus*) have led to rapid declines in native species on islands throughout the Pacific [32].

Enhancing macroecology by drawing on behavioural ecology

Macroecology is an approach that brings together multiple disciplines to reveal and explain repeated patterns in the abundance, diversity, and distribution of life on Earth [7,11,33,34]. It aims to identify properties of ecological entities (e.g., communities) that emerge from the relative noise of many individual components (e.g., species), and understand the processes that generate and maintain those properties [7,11,34]. Macroecological questions are diverse and include those directed towards understanding the relationship between life history strategies and extinction risk; assembly rules for local communities from regional species pools (e.g., neutral models); allometric scaling relationships such as body size and speciation rates; and geographic patterns in species diversity and abundance [35]. One element that is largely missing from explanations of macroecological patterns and processes is the explicit consideration of behaviour, potentially leading to spurious results. For example, behavioural flexibility and species interactions were shown to be essential components to generate accurate species distribution models for Alpine chamois (*Rupicapra rupicapra*) [36]. Therefore, at this other end of the spectrum, we believe it is

Box 2. Eco–evo models and the Red Queen hypothesis

Classical behavioural ecology theory takes population persistence as a given, which limits its utility for explaining patterns above the population level and for predicting responses to environmental change. Relaxing this assumption can yield important insights about the relevance of behaviour for species coexistence, and by extension, larger scale patterns. Grether and Okamoto [68] used an individual-based model grounded on the life cycle of territorial birds to examine whether selection could rescue a superior interference competitor from extinction without driving a superior exploitative competitor extinct, and vice versa. Their eco–evo simulations showed that coexistence was possible over a wide range of ecologically plausible scenarios, and up to the highest levels of resource overlap, but only if the species continually coevolved (Figure I). One implication is that reductions in population size and genetic variation could destabilise coexistence between territorial species.

We believe a generalised version of this model might help explain a large-scale pattern in the fossil record, namely that for most groups of organisms the probability of extinction is independent on the age of a taxon [69]. To explain the pattern, Van Valen [69] famously proposed that competing species can only increase in fitness by evolving at the expense of each other, resulting in a zero-sum (Red Queen) game in which none of the species increases in fitness over the long term. While Van Valen framed it in group selection terms, Grether and Okamoto [68] showed that a similar zero-sum game can emerge from individual-level selection.

Whether eco–evo models can be scaled up to test mechanistic explanations for emergent macroecological patterns is an open question (see Outstanding questions). It may be that fundamentally different processes operate at different spatial and temporal scales (e.g., demography and individual-level selection at local scales and species sorting and species-level selection at regional scales) [7]. However, purely ecological (Lotka–Volterra-based) models have been used with some success to reproduce well-documented macroecological patterns [70,71]. In principle at least, modelling approaches that explicitly account for behaviour and allow species to evolve in response to each other could prove useful for evaluating whether macroecological patterns are likely to arise from microscale processes.

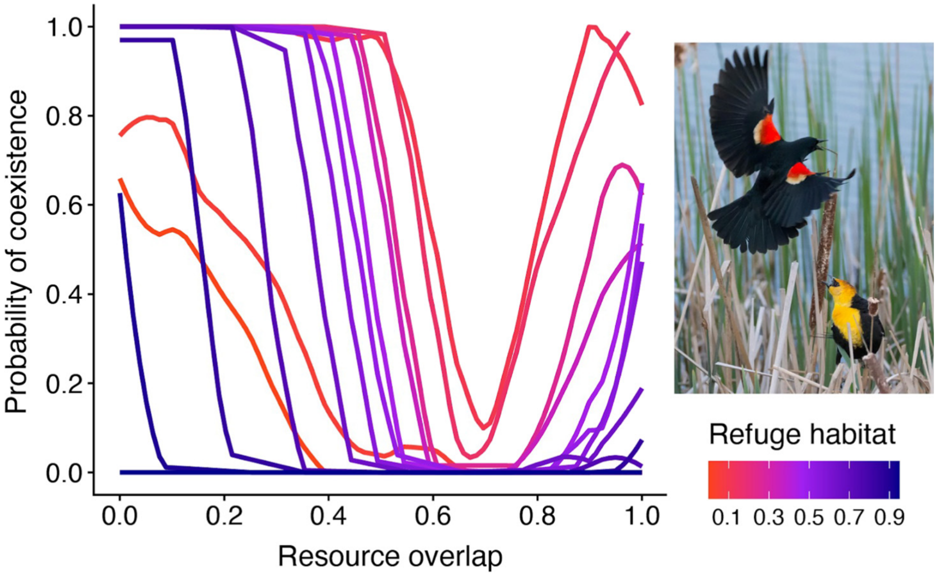

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Figure I. Probability of coexistence under territoriality. Coexistence depends on resource overlap and the fraction of the habitat where the superior resource competitor could breed without interference from the superior interference competitor. For further details, see Grether and Okamoto [68]. Inset photo: territorial fight between red-winged blackbird (*Agelaius phoeniceus*) and yellow-headed blackbird (*Xanthocephalus xanthocephalus*) on a marsh in British Columbia, Canada. Photo credit: Feng Yu / Alamy Stock Photo (with permission).

beneficial to incorporate behaviour explicitly as an underlying mechanism. For instance, territorial behaviour is a key predictor of tropical bird species' elevational range limits [37,38], highlighting the importance of incorporating behaviour when forecasting altitudinal range shifts under climate change [5].

Rapid behavioural change mediates top-down drivers

Hypotheses to explain macroecological patterns in abundance, diversity, and distributions abound, with >100 hypotheses aiming to explain the latitudinal diversity gradient alone [39]. Macroecological hypotheses tend to involve top-down processes that operate over long time scales, such as selective colonisation driven by plate tectonic movements [40,41], differences in speciation rates [42], and relationships between body size and metabolism [43]. By contrast, behavioural change can be rapid, on the scale of days, and is often the first response of individuals to both acute and chronic disturbance in a world of human-induced rapid environmental change [1,5]. For example, temperature tolerance as a predictor of species geographic range distributions is modified strongly in terrestrial ectotherms by fine-scale behavioural thermoregulation [21,44]. Understanding the role of behaviour in mediating these top-down processes is likely to be increasingly important.

Predicting the future of biodiversity requires context

To achieve its aim of generalisability, macroecology requires data across large geographical, taxonomic, or temporal extents, but it can be challenging to measure all potentially relevant variables. The omission of behavioural and physiological variables was acknowledged at the inception of macroecology to be '...more a matter of practicality than philosophy…', and it was suggested that '...the morphology, physiology, and behaviour of individual organisms play major roles in causing, or at least constraining large-scale patterns of distribution and abundance, both within and among species.' [33]. It is now increasingly recognised that ecological outcomes are context-dependent, and that in many cases, taking behaviour into account is necessary to understand context dependency [4]. Without this level of detail, we may be unable to predict species responses into the future, highlighting the need to take a more mechanistic approach [7,24]. For example, the addition of feeding behaviour to data on abundance and temperature predicted diminished trophic interactions for reef fish in response to global warming, highlighting the potential loss of critical ecosystem functions by 2050 [45].

Asking new questions

The true integration of these disciplines is where questions are posed with the explicit recognition of both disciplines from the outset (Figure 1 and Figure 2 middle of spectrum). We offer a schematic to think through how a given behaviour, here **territoriality**, might interlink with the four key macroecological processes (Figure 1 and Box 2). Some of these questions draw on established hypotheses or theories from one or both disciplines, while others are more exploratory and aimed, in the first instance, at quantifying patterns. While we talk about these questions as new, we note that Brown [33] used allometry to develop hypotheses that linked body size, geographic range size, population density, space use, and territoriality, predicting increased territoriality in modal-sized species. Therefore, rather than claiming all questions in this space are new, it is more accurate to say that some are resurrected, some will coalesce, and some are yet to be asked.

Although scarce, macrobehavioural studies have been carried out on each major axis of scale. At a large spatial scale, geographical gradients in intraspecific lethal aggression in mammals could be predicted by photoperiod seasonality, leading to the hypothesis that variation in lethality across mammalian assemblages is driven by hormonal control [46]. At a large taxonomic scale, the characteristics of sickness behaviours and their potential implications for disease spread were explored across the five vertebrate classes [47]. One finding was that fever is triggered by similar molecular pathways in both ectotherms and endotherms despite differences in how body temperature is regulated (i.e., behaviourally vs. physiologically), suggesting that fever is highly adaptive. Finally, at a large temporal scale, behaviour of skinks (*Lampropholis delicata*) was shown to diverge from native counterparts after invasion of new localities in the Pacific Ocean, leading to greater individual plasticity and lower inter-individual variation on invaded islands [48]. All these examples deliver new fundamental insight into behavioural variation across space, taxa, and time, as well as generating results with ramifications for conservation.

While we largely focus here on leveraging spatial and relatively shallow (i.e., decadal) temporal variation in behaviour to test hypotheses, we can also examine variation over deeper timescales (i.e., millions of years). Macroevolutionary approaches have been used to illuminate the pathways through which behaviours arise (e.g., tail vibration pre-dated the evolution of rattles in rattlesnakes [49]) as well as the ways in which behaviours have themselves impacted rates of speciation (e.g., migratory behaviour leads to high speciation rates resulting from the evolution of sedentary daughter lineages [50]). These examples suggest that a merger of behaviour and macroevolution may yield similarly valuable insights as a merger of behaviour and macroecology (e.g., see speciation and extinction in Figure 1). The boundary between macroecology and macroevolution is often blurred and we encourage similar vision here.

Conservation relevance

The difficulty of linking large-scale patterns to underlying mechanisms has hampered the application of macroecology to conservation problems [51], while it is often difficult to extrapolate behavioural ecology beyond the system in which results were obtained. As behaviours respond plastically to buffer the effects of environmental change, or species fall into ecological traps, the way behaviour mediates ecological patterns and processes at large scales in space, time, and taxa will become increasingly visible and critically important as a consideration for conservation [5,52]. It is our hope that macrobehaviour can improve integration of both macroecology and behavioural ecology into conservation.

From a macroecology perspective, geographical and ecological traits can be used to infer species vulnerability. Estimates of bird extinction risk were improved with the addition of behavioural traits such as foraging strategy, suggesting that integrating behaviour into global conservation strategies is desirable [53]. Priority areas were identified as targets for light pollution mitigation to reduce potential disruption to migratory behaviour using global maps of 298 routes for nocturnally migrating bird species combined with light pollution maps from satellite data [54,55]. Integrating the presence of vocalisations via acoustic monitoring data into species distribution models can indicate suitability of a location for reproductive, territorial, and predation behaviour, bolstering information on the suitability of environmental conditions [56].

Behaviour can offer an early indicator of future changes to population dynamics [57] and could potentially be applied geographically to identify and triage at-risk populations. For instance, effects of fishing on shoaling and reproductive behaviour are anticipated to have repercussions through trophic food webs, with ramifications for local economies [58,59], potentially affecting human wellbeing if subsistence fisheries become less efficient.

Moving forward with macrobehaviour

Moving forward with this research agenda will require cross-disciplinary collaboration and data. Teams must bring together expertise in both disciplines, and perhaps most importantly, a willingness to listen and learn from one another. We hope that over time, macrobehaviour will move from multidisciplinary to true interdisciplinary research, asking new questions and tackling them with skills drawn from across the disciplines. In particular, we must begin to disentangle how selection interacts iteratively with macroecological processes of movement, maintenance, speciation, and extinction, and to tackle methodological and conceptual challenges inherent to scaling up.

The biggest challenge to conducting macrobehavioural research is generating the data required to test hypotheses at scale. Nevertheless, there are several ways forward, including open-access databases, globally distributed experiments, observational approaches (Box 1), and modelling techniques (e.g., individual-based simulations) (Box 2). It is also advantageous to recognise that one set of behavioural data collected across large scales can provide fundamental insight for both macroecology (e.g., how behaviour influences range distributions) and behavioural ecology (e.g., stronger tests of theory) simultaneously. For some questions, it could be that existing behavioural data can be compiled from online sources, whilst other questions will require collection of primary for-purpose data [60]. Brown [33] notes that experiments must be replicated in multiple localities, and preferably habitats, if we are to reach generalisable conclusions.

Concluding remarks

Macrobehaviour offers a new field to unite the disciplines of behavioural ecology and macroecology. It is particularly pertinent in an era of rapid environmental change where behavioural change is often the first response to altered conditions. Macrobehaviour offers a spectrum of involvement where researchers can draw on as little or as much as they wish from the less familiar field, ultimately reaching questions that would not be asked without the explicit consideration of both disciplines (see Outstanding questions). This can lead us towards new fundamental insights that have the potential to be relevant for conservation action, making it imperative that we coordinate efforts and share knowledge to push these frontiers forward as fast as possible. Fully linking behaviour to macroecological scales will require investigations of transmutation and emergent properties, and explicit recognition that selection operates against a backdrop of differential speciation, extinction, and movement. We hope that by uniting existing work and encouraging new research in this area, we can learn from one another more easily and new coherent lines of inquiry can be developed and tested.

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Declaration of interests

No interests are declared.

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Outstanding questions

Conceptual

Which behaviours are most likely to vary geographically and why?

How can variation in behaviour structure biogeographic patterns of species distributions, abundance, and diversity?

How do different behaviours scale allometrically, for example, with body size?

What is the importance of behaviour relative to other factors in structuring macroecological patterns?

Are there fundamental differences in behavioural variation in different biomes and/or ecosystems, and how can any such differences be explained?

Can ecoevolutionary models (e.g., of species interactions) be scaled up to test mechanistic explanations for macroecological patterns?

Can data on the behaviour of extant taxa be used to test explanations for patterns in the fossil record, such as the original Red Queen hypothesis?

Can sound inferences be drawn from macroecological patterns about the behaviour of the component taxa?

Methodological

Which macroecological approaches are most useful for testing theories and hypotheses from behavioural ecology?

What are the advantages and disadvantages of different methods (e.g., collating existing data from literature, primary data collection) for collecting behavioural data for macroecological questions?

How far can we make dual use of behavioural data for both behavioural ecology and macroecology in the same study?

How can we standardise collection of behavioural data for use in macrobehaviour? What details are we willing to trade-off to achieve generality?

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How do we best initiate and consolidate collaboration across disciplines?

How do we avoid statistical pitfalls when scaling up?

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