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Opinion

Usefulness of Species Traits in Predicting Range Shifts

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Information on the ecological traits of species might improve predictions of climate-driven range shifts. However, the usefulness of traits is usually assumed rather than quantified. Here, we present a framework to identify the most informative traits, based on four key range-shift processes: emigration of individuals or propagules away from the natal location; the distance a species can move; establishment of self-sustaining populations; and proliferation following establishment. We propose a framework that categorises traits according to their contribution to range-shift processes. We demonstrate how the framework enables the predictive value of traits to be evaluated empirically and how this categorisation can be used to better understand range-shift processes; we also illustrate how range-shift estimates can be improved.

Trends

The ecological traits of species are increasingly used to inform predictions of climate-driven range shifts.

Traits utilised should correspond to range-shift processes: emigration, movement, establishment, and proliferation. We categorise traits according to the information that they offer for each process.

The most informative traits can be informed by biogeographical and demographic evidence bases: species range sizes, range filling, recent range shifts, population fluctuations, and success following naturalisation.

Movement traits are often used in range-shift studies, although their importance is not universally supported. Ecological generalisation, persistence in unfavourable conditions, reproductive strategy, and intraspecific competitive ability should be considered for inclusion in range-shift evaluations.

Predictive Traits as a New Paradigm in Climate Change Ecology

Mitigating the threat from climate change to biodiversity and ecosystems requires a robust understanding of how species will respond to new climatic conditions. The most common method for estimating the exposure of a species to climate change is to compare future climatic conditions against the conditions in which the species currently lives [1]. While there is disagreement about the accuracy of these techniques, they are well explored, and there is literature on best practice [2,3]. Species vulnerability to exposure is less well understood. A major uncertainty is whether species are able to colonise newly climatically suitable areas as current geographic ranges become unsuitable. Such '**range shifts'** (see Glossary) could mitigate threats from climate change.

Predictive traits ('Indicative' or 'Life-history' traits) have been suggested as a simple way to improve estimation of the range-shift capacity of a species, identifying how well a species is likely to cope with climate change [4–7]. 'Range-shift capacity' could be interpreted as the likelihood of range shifts occurring or the timescale over which range shifts might occur. The emerging approach is to integrate information on both the exposure of a species to climate change and the traits expected to drive range-shift capacity, producing a relative metric of species risk [4–6]. Quantitative evidence is rarely used to inform the choice of predictive traits in these approaches, and trait selection often relies on expert opinion and data availability [4,6]. There is no consensus as to the traits that should be considered in range-shift forecasts, meaning that studies are not comparable and that trait data could obscure rather than clarify climate-change threats. Consequently, there is need to quantify how different traits contribute to species range shifts and to identify potentially informative traits for which we do not have sufficient information.

A Framework to Evaluate and Use Predictive Traits

The framework that we propose here permits the use of existing evidence bases to identify the most important traits and range-shift processes for a given taxa, improved testing of the relation

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between traits and range shifts, and superior assessments of the range-shift capacities of large numbers of species. Given the hundreds of traits that could be analysed for different taxa, this framework would enable future studies to be comparable. In addition, while the evidence bases we discuss are correlative, choosing traits to analyse based on our framework would generate testable hypotheses as to causal mechanisms.

In addition to climate-change ecology, bodies of theory within metapopulation, invasion, **life-history**, restoration, and reintroduction ecology deal with range shifts, that is, the **establishment** and expansion of new populations. We draw from these disciplines to identify four key range-shift processes (Box 1). Despite widespread acceptance of these range-shift processes, their importance for any given taxa or range-shift scenario is poorly known. Traits could be used to indicate the likelihood that each range-shift process will occur successfully but the relevant traits are numerous and diverse, will differ between taxa, and some are poorly quantified for many species. This presents difficulties for evaluating the importance of a given trait. Therefore, we propose a trait categorisation (Box 2) that corresponds to range-shift processes. This categorisation results in testable hypotheses as to causal mechanisms underlying the relation between traits and range shifts. The categorisation also allows trade-offs and interactions between traits to be recognised and accounted for. For example, migratory status could affect range-shift capacity positively by conferring high **movement ability**, or negatively by limiting **emigration** because migrants show fidelity to breeding and overwintering sites between years [8,9] (Box 2). Indeed, species with migratory ability have been noted to have low range-shift potential [10], possibly because migrants show site fidelity (Table 1). We demonstrate how the framework could be applied to improve range-shift predictions in Box 3.

In addition to traits, various range-shift stages might be affected by a species' level of exposure to climate change and, thus, by the species' climatic tolerances. Here, we deal exclusively with how traits can be used to improve range-shift predictions, but raise the aforementioned issues in the Outstanding Questions.

Evidence Bases for the Relevance of Predictive Traits to Range-Shift Capacities

There are multiple metrics for which a wealth of data exists that can be used to evaluate the predictive value of traits. Traits that correlate with biogeographical patterns and their changes

Box 1. Range-Shift Processes

The first range-shift process (Figure I) is that individuals embark on a journey away from their natal location (emigration). For animals, the motivations involved include high population density, low resource availability, and harassment from prospective mates [45]. For sessile taxa, such as plants, some aspects of reproductive behaviour can affect the probability that propagules disperse away from the location of the adults; for example, timing of seed shed to maximise dispersal by animals [53]. Species that have a physical or behavioural mechanism that promotes emigration are more likely to respond to poor environmental conditions (as driven by climate change) by leaving the natal location than those that do not have these mechanisms. Recent applications of metapopulation modelling approaches to climate change highlight the importance of emigration for range shifts [45,54]. Movement itself (i.e., the transfer of individuals or propagules away from the location in which they originated [54]) is the second and most widely studied range-shift process. The upper limit of the dispersal distance of a species is one of the strongest limitations to metapopulation persistence, invasive spread, and population recovery [55–57]. The third range-shift process is establishment (i.e., the ability of dispersing individuals to reproduce and found new populations following a dispersal event). While the probability of establishment is affected by the number of arriving propagules at a site, dispersal, invasion, and reintroduction ecology demonstrate that nonmovement traits and their interaction with local conditions also mediate ease of establishment [58]. The fourth range-shift process is proliferation (i.e., the growth of established populations to become more than self-sustaining, producing individuals that will in turn disperse and cause further population spread [59]). In the short term, spreading outwards to locations immediately surrounding the newly colonised location will improve population robustness. In the longer term, a large number of emigrating individuals will sustain the range shift itself. Life histories that permit rapid proliferation contribute greatly to the long-term success of naturalised and reintroduced populations [47]. Predictive traits used in climate-change risk assessments should correspond to all of the above processes.

Glossary

Area of occurrence (AOO): the geographic area that is occupied by a species [48], often defined as the number of occupied grid cells (which vary in size between atlases) [20].
Competitive ability: the ability of an individual of one species to reduce the availability of contested resources to an individual from another species, and to tolerate or avoid reduction in contested resource availability by an individual from another species [49].
Ecological generalisation: the ability to use a variety of a given resource type; for example, ecological generalists could breed in a variety of land-cover types, have a broad diet, or tolerate a broad range of soil types.
Emigration: first range-shift process in which an individual embarks on a journey (movement) outside its natal location.
Establishment: range-shift process following movement, in which one or more individuals reproduce and found a self-sustaining population.
Extent of occurrence (EOO): the area within the outer limits of the geographic distribution of a species [43,48].
Indicative traits: characteristics of a species related to environmental tolerance, habitat specialisation, geographical boundaries, or spatial distribution [5,7,50]. These traits can be measured at the individual or population level and, therefore, are not life-history traits in the strict sense.
Life-history traits: morphological, physiological, or phenological characteristics measurable at the individual level that have an effect on individual performance [51].
Movement ability: ability of an individual or propagule to travel outside its natal location. This ability is often represented as the average or upper end of the distance moved in the lifetime of an individual or propagule. Note that this can be informed by, but is not restricted to, natal dispersal distances (movement from natal to breeding site). We specifically use 'movement ability' instead of 'dispersal ability' to avoid confusion, because the latter is widely used to include emigration, movement, and establishment [52]. The movement process in dispersal has also been called transience, transport, and transfer [52].