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Biogeographic concepts define invasion biology

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Biological invasions, although mechanistically related to other causes of rarity and abundance, are distinct in that they arise through human-mediated extra-range dispersal [1]. This difference in origin affects how we understand and manage all categories of introduced organisms [2]. The logical extension is that invasive organisms should be defined in biogeographical terms.

The movement of species across biogeographical barriers by humans has ecological and evolutionary consequences directly related to the dispersal pathway and the differences between the native and non-native ranges [1,3]. This has given rise to several core concepts in invasion biology, e.g. natural enemy release and biotic resistance. These concepts can, and are, used more generally to assess the effects of major exogenous modifications to the environment. But while biological invasions, climate change and habitat destruction have complex interactive effects on many organisms, in our view the study of biological invasions remains the study of a special case of population dynamics. Such research should consider both the effects of human-mediated dispersal of organisms to new biogeographic regions, and the consequences of these introductions—how organisms survive in transit, establish, naturalise and spread, either immediately or often after a lag phase.

For example, while the demographics of range expansion of *Sturnus vulgaris* (starlings) in Europe and their invasion of North America are comparable, the limitation to spread in North America was initially biogeographic (starlings were brought there by humans), whereas in Europe there was biotic resistance (starlings were only able to spread after humans had altered the habitat). This distinction can and does have direct, measurable and predictable consequences (e.g. on evolutionary potential [3–5]).

Valéry *et al.* [6] discuss two additional ways of defining biological invasions. We agree with their arguments as to why defining biological invasions in terms of impact is problematic [1,7]. However, they also argue against the biogeographical definition, proposing instead a third definition: they suggest the term 'invasive' should refer to species that acquire a competitive advantage in a new area, following the disappearance of natural obstacles to

their proliferation. We agree with the need for neutral terminology [8], but there is a large existing lexicon to describe organisms that reach ecological dominance [9]; and, in our view, this proposed definition does not clearly circumscribe a concept. Are some cicada populations invasive one year out of 17? Or are they restricted by 'natural obstacles'? The permanence of ecological dominance is not guaranteed, neither is the permanence of invasive populations [10]. The definition by Valéry *et al.* [6] merely shifts the uncertainty inherent in any definition at the expense of our ability to describe a unique concept.

Biological invasions are a special type of range expansion. We believe that conceptually separating invasive and native organisms is important both for successful natural resource management and when developing and testing ecological theory.

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