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Climate-tracking species are not invasive

Applying an invasive framework to native species that are shifting their ranges in response to climate change adopts an adversarial, local and static paradigm that is often at odds with protecting global biodiversity.

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Climate change is already altering local species abundances, affecting ecosystems, inducing extinctions and shifting species ranges along elevational and latitudinal gradients[1,2]. Biologists and managers increasingly must decide how to protect biodiversity and ecosystems from climate change, including when and how to preserve local populations and what

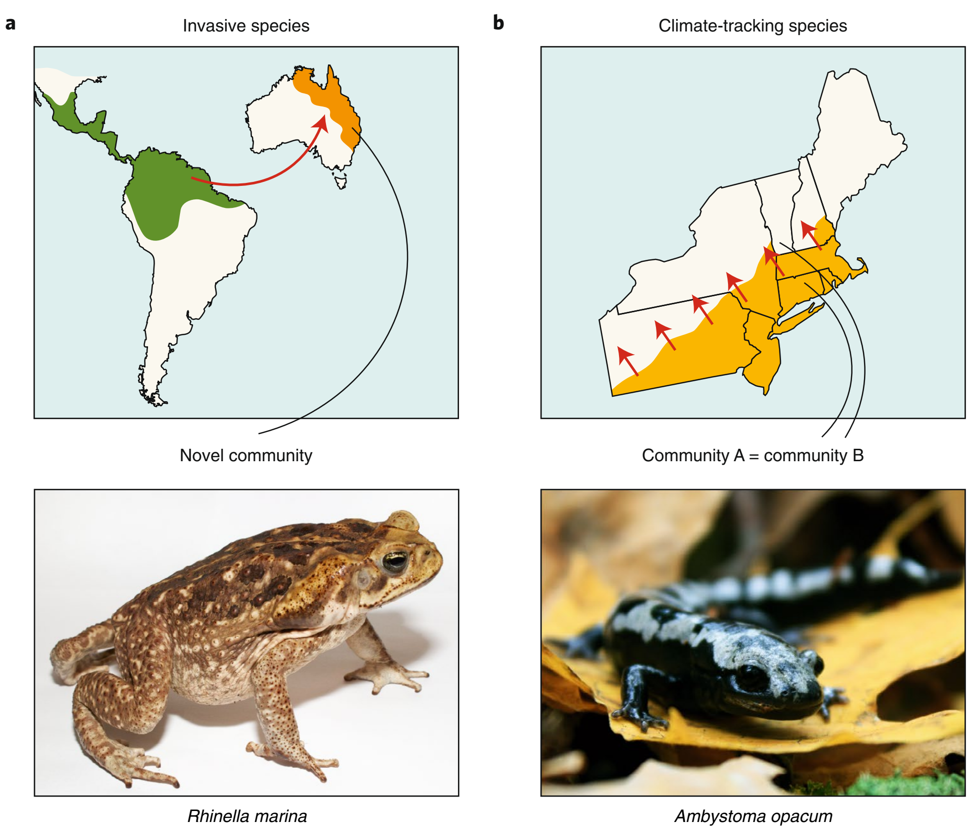

Fig. 1 | Invasive and climate-tracking species differ in geographic origins, which influences their expected effect on new ecosystems. a,b, Invasive and climate-tracking species differ in whether their origins are distant or adjacent to their new range, which determines the degree to which they will interact with novel environments and species as well as their potential ecological impact. The cane toad (*R. marina*) (**a**) was transported to Australia from its native range in South and North America. In Australia, it encounters novel environments and naïve species and substantially threatens native ecosystems. In contrast, the marbled salamander (*A. opacum*) (**b**) is expanding its range northward in response to climate change. Because it colonizes adjacent habitats, it encounters more similar environments and the same species as in its original range. Although it, too, has substantial impacts on recipient communities, these impacts are similar to those observed in its current range. Thus, its expansion can be viewed not as an invasion, but as the expected northward movement of an existing and intact community.

to do about new species arriving via climate-induced range shifts[3,4]. One approach (for example, see ref. [5]) is to adopt insights developed for invasive species and apply them to species shifting their distributions in response to changing climates (hereafter referred to as 'climate-tracking species'). Although it is tempting to draw comparisons between climate-tracking and invasive species, here I will discuss the flaws in this analogy and how its application may even threaten efforts to conserve global biodiversity.

Invasive species constitute one of the top threats to biodiversity and ecosystems worldwide[3]. Although sometimes applied more broadly to include native species, invasive species are usually defined as organisms that humans establish far outside their native range and which negatively affect recipient communities and ecosystems[6,7]. This commonly used definition combines both distant origins and strong ecological impacts, recognizing that species from more divergent biogeographical origins usually cause the greatest impacts on recipient ecosystems. These negative impacts stem from invasive species' unique traits not found in recipient communities, lack of a shared evolutionary history with native species and potential release from native competitors and enemies in the introduced range. Climate-tracking species, in contrast, expand from native distributions into adjacent regions recently made habitable by climate change and often do not substantially affect recipient communities.

On the surface, applying our extensive knowledge about invasive species to climate-tracking species seems logical. Both invasive and climate-induced range shifts result from human disturbances. Both shifts can produce no-analogue communities, alter communities and ecosystems substantially, and cause local extirpations. However, the differences between the two dynamics are extensive, thus rendering the analogy less useful in the end.

First, invasive species originate from spatially and often biogeographically distinct regions, such that invasive species experience novel environments and biological communities in their introduced range. For instance, humans transplanted cane toads (*Rhinella marina*) from America to Australia, where no native toads existed, and they now cause extensive damage to Australian wildlife[8] (Fig. 1a). Climate-tracking species, in contrast, expand from adjacent native populations into largely similar environments. Although no-analogue species interactions can occur during these range shifts[9,10], climate-tracking species often interact with many of the same species in their expanded range, either because these species are moving with them or because they already occurred there. For example, the marbled salamander (*Ambystoma opacum*) is expanding its distribution in New England, USA, in response to warmer winters. In anticipation of its northward spread, I sampled habitats north of its current range where it might expand in the next decade and found the same amphibian and macroinvertebrate species that occur in the marbled salamander's current range (Fig. 1b). Although climate-tracking species might initially outpace their enemies, these enemies are local and will likely catch up, setting the stage for transient, rather than permanent, impacts. In contrast, the distant enemies of invasive species might never arrive.

Second, unlike invasive species, range-shifting species will generally interact with species and environments with which they have a longstanding or previous evolutionary history. No-analogue communities sometimes form during historic shifts in species distributions[11,12], and these species that coevolved together historically might still retain some capacity to coexist if climate change brings them back together. For example, prey often recognize and respond defensively to predators that they encountered long ago in the past (for example, the 'ghost of predation past'[13]). Also, gene flow from nearby, experienced populations might provide the genetic material for naïve populations to adapt quickly to a climate-tracking species and thereby mediate its negative impacts[14]. Thus, evolutionary history and contemporary gene flow can lessen the ecological impacts of climate-tracking species in contrast to invasive species, which usually lack a shared evolutionary history with recipient community members.

Third, different traits predict invasiveness and climate tracking. An expansive literature has uncovered a large suite of traits that predict the invasiveness of introduced species. These traits include rapid growth, fast generation times, high offspring production, characteristics facilitating human and animal dispersal, wide niche and diet breadth, and resistance to human disturbances, to name a few[15,16]. In contrast, no consistent set of traits predicts the extent of range shifts in response to climate change. For climate change responses, the best predictive factors were biogeographical patterns rather than traits (such as range size and historical limits), and even these significant factors explained little of the total variation in climate tracking[17,18]. Instead, other factors, such as biotic interactions, which are not captured easily by generalizable traits, might be mediating variable responses to climate change[17]. Thus, trait-based approaches inferred from species invasions have not been useful in predicting climate change responses.

Fourth, adopting an invasive species framework for climate-tracking species associates native species with the language and culture of eradicating invasive species. Conservationists and land managers routinely 'battle' invasive species, and some invasive species are likened to national security threats. Language in conservation biology can bias how we think about issues and make decisions[19]. Even casual references to invasive species will place native, climate-tracking species in the same category as non-native species that must be controlled and eradicated rather than protected and facilitated in their responses to changing climates.

Fifth, and most importantly, applying perspectives from invasion biology to climate-tracking species preserves local, historic patterns and arbitrarily chooses local winners over colonizing losers, thereby threatening species and ecosystems at broader regional and global scales. The same climate-tracking species arriving and disrupting a local community might also be threatened in their original range. Preventing shifts in species and ecosystems in favour of local, historic patterns is not only likely to be futile, but could cause range collapses or extinctions at broader scales. We want species to shift their distributions along climate gradients to maintain existing biodiversity and ecosystems, even if they become spatially displaced. Natural range shifting is an important, effective and cheap form of ecological resilience. Rather than blocking range-shifting species as suggested by the invasion paradigm, we should be facilitating the movement of poorly dispersing species to keep entire communities intact and functioning. As the world warms, local conservation strategies must operate at larger scales, and decision makers should accept that, if everything goes well, their local ecosystem will eventually look a lot like those located in warmer regions, just as their ecosystem will replace those in cooler regions.

A better approach is to build a framework informed by insights particular to climate-tracking species. Building a decision framework focused explicitly on the challenges of climate change rather than borrowing from invasive species research would enable the important insights needed by conservation efforts without stigmatizing the species lucky enough to have the capacity to keep pace with changing climates. Our current inability to predict which species can best track climate change[17] suggests the need for a deeper observational and experimental inspection of climate-tracking species and strategies to best predict their sensitivities to climate change and impacts on recipient ecosystems. The invasive species paradigm offers some lessons about species impacts on recipient ecosystems, but more specific theories exist and should be developed that pertain specifically to climate-tracking species[20]. Another challenge is how best can we support shifts of entire species assemblages, especially for the poor dispersers and rare or endangered species. Additional avenues for exploration include assessing the role of divergent species interactions, ecological and evolutionary debts, interactions between land use and climate change, and eco-evolutionary feedbacks in determining climate-induced range expansions.

Efforts to build a framework for climate-tracking species based on their unique traits and challenges will facilitate more effective conservation efforts that treat these species as they should be treated: not as invasive species to keep out, but rather as the refugees of climate change that need our assistance. To rob them of their natural resilience is to frustrate larger efforts to maintain biodiversity and ecosystem function. During climate change, we should keep nature alive, even if it happens to be in a different place. ❐

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