

Opinion

Community Assembly Theory as a Framework for Biological Invasions

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Biological invasions present a global problem underlain by an ecological paradox that thwarts explanation: how do some exotic species, evolutionarily naïve to their new environments, outperform locally adapted natives? We propose that community assembly theory provides a framework for addressing this question. Local community assembly rules can be defined by evaluating how native species' traits interact with community filters to affect species abundance. Evaluation of exotic species against this benchmark indicates that exotics that follow assembly rules behave like natives, while those exhibiting novel interactions with community filters can greatly underperform or outperform natives. Additionally, advantages gained by exotics over natives following disturbance can be explained by accounting for extrinsic assembly processes that bias exotic traits toward ruderal strategies.

The Need for an Overarching Framework to Guide Invasion Ecology

Human-assisted translocations of biological organisms have enhanced societies around the globe by increasing the availability and diversity of foods, medicines, and construction materials and generally enriching our lives [1]. However, a subset of organisms that are introduced by humans, intentionally or otherwise, become established within and transform native ecosystems, disrupting ecosystem services provided to humans [2]. Such **exotic** (see [Glossary](#)) species have become a leading threat to native species and natural systems around the world [2,3]. They also present an ecological paradox: how do some exotic species, presumably evolutionarily naïve to their new surroundings, outperform locally adapted natives [4]? Deciphering this paradox is critical to managing and mitigating invasions. Yet, despite an explosion in research on this topic over recent decades [3], we still lack a general explanation for the invasion paradox. Invasion ecology has become mired in a debate regarding whether exotic species behave any differently than natives [3], despite the fact that many exotic organisms have overrun recipient **communities** to become some of the most notorious pest species around the world [3,5]. We contend that progress in invasion ecology has been hindered by the lack of an overarching framework capable of integrating the key pieces of the invasion puzzle and organizing the field into a more directed science. Here we explore the potential for community assembly theory – the theoretical framework originated to explain the organization of native communities [6,7] – to serve as a framework for integrating and advancing invasion ecology.

Dozens of hypotheses have been proposed to explain invasion outcomes [8–10]. These hypotheses offer *ad hoc* explanations for specific invasion scenarios but none provides an overall explanation for the full range of invasion outcomes. For example, the enemy release [11] and novel weapons [12] hypotheses offer mechanisms to explain why some exotics become **invasive** pests (invasiveness) due to changes in biogeographic context (the role of **provenance**), but they do not explain why so many others fail to become problematic when

Highlights

We build on recent studies to demonstrate how community assembly theory can provide a framework for advancing invasion ecology.

In this framework, the success of exotic species in recipient communities is determined by how their traits interact with local ecological filters.

This approach illustrates that most exotics follow community rules to become naturalized species that behave like the natives; that is, traits predict their abundance according to local rules as they do for natives. However, some exotics can underperform or outperform relative to the natives when they exhibit novel interactions with local filters due to their unique ecological–evolutionary histories.

This approach also illustrates that the widely noted advantage of exotics over natives following disturbances can arise when extrinsic filters bias local exotic species pools toward traits that facilitate invasiveness.

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introduced (the **context dependence** of invasiveness). The fluctuating resource hypothesis (FRH) [13] addresses the pervasive role that disturbance plays in affecting community **invasibility**, but it does not explain why disturbance tends to increase the susceptibility of communities more to invasion by exotic than by native species [14,15] (the role of provenance). The biotic resistance hypothesis [11] postulates that many introduced species fail to establish or become problematic pests due to negative interactions with native species, but it does not explain why some exotics might bypass such resistance to prosper even in highly resistant communities. More generally, the interplay between species invasiveness and community invasibility requires better integration [16–19]. Notably, some exotics become serious pests in one community but fail to do so in others [20], indicating an important role of community context in invasions [16,21–23]. In sum, individual invasion hypotheses offer explanations for specific invasion outcomes, but only in aggregation can they begin to explain the full range of invasion outcomes. To develop a comprehensive understanding of **biological invasions**, we need a means of organizing invasion hypotheses to address the key invasion elements and research gaps highlighted above.

A comprehensive conceptual framework for biological invasions should address the following: (i) explain invasiveness (i.e., explain the success of invaders within the recipient community, from failure to colonize to naturalization or achievement of pest status, and the role that invader traits play in these outcomes); (ii) integrate provenance effects to explain how species' origins can influence invasion outcomes; (iii) organize invasion hypotheses to link each one to the specific outcomes it proposes to explain; (iv) explain invasibility (i.e., the processes influencing the susceptibility of communities to invasions); and (v) address the context dependence of invasions. The need for an overarching framework capable of synthesizing the field of invasion ecology has been echoed by many invasion scientists [22,24–36]. Successive invasion frameworks have increasingly extended our insights by capturing key components of the invasion puzzle [22,24–36], but we still lack a framework capable of incorporating all of the essential elements above in a way that fully integrates this field.

A Brief Introduction to Community Assembly Theory

Community assembly theory originated as a biogeographic approach to explain island bird assemblages [37] that was later adapted as a general framework for understanding the structuring of natural communities [6,7]. This longstanding theory is increasingly recognized as a viable framework for unifying ecology [38] due to its ability to integrate emerging evolutionary and ecological concepts ranging from large-scale neutral processes and environmental filtering to small-scale, niche-structuring, and demographic processes [39–42]. For similar reasons, community assembly theory holds potential for the integration of invasion ecology. According to community assembly theory, the composition and relative abundance of species within a community is determined by a series of hierarchical filters that allow or impede the passage of each prospective community member based on its functional traits [6]. Heuristically, assembly processes are assigned to discrete filter levels (Figure 1), but dispersal processes can influence all levels of assembly to some degree. Importantly, **extrinsic** processes associated with the global species pool and dispersal filter determine the type and abundance of biological units arriving at the local community, where **intrinsic** abiotic and biotic processes sort these incoming biological units to determine final community composition and relative abundance.

In practice, the function of specific intrinsic filters can be determined by evaluating how variation in a functional trait or trait set influences the relative fitness of prospective community members. Here, we distinguish species-level fitness, measured by species abundance, from evolutionary or

Glossary

Biological invasions: colonization of communities by species that did not originate or evolve therein due to natural dispersal barriers. Such events are often human facilitated and intercontinental or transcontinental but can involve introductions across regional or local barriers.

Community: an assemblage of populations of two or more species interacting within a specific geographic area. We use this term in reference to 'community types' defined as units of similar community structure (composition and relative abundance) repeated across similar physiographic conditions.

Context dependence: variability in processes linked to changes in abiotic and/or biotic conditions.

Exaptation: a trait that now enhances fitness but was not built by natural selection for the current role [76].

Exotic: organisms introduced, often by anthropogenic means, into communities where they did not naturally occur.

Extrinsic: factors or processes acting from outside a community.

Intrinsic: factors or processes originating from within a community.

Invasibility: the susceptibility of a community or location within the community to invasion by outside species (exotic or native).

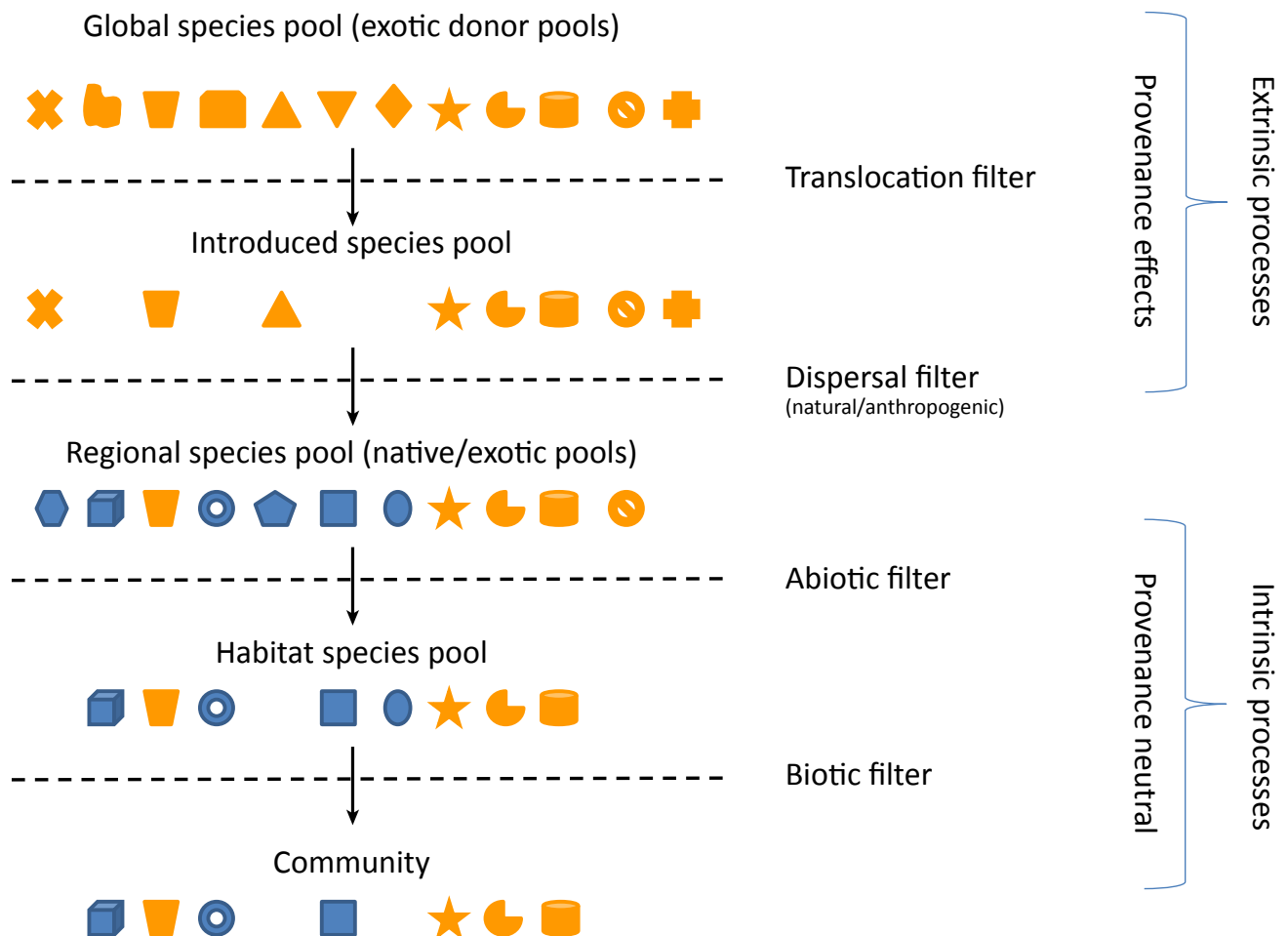
Invasive: the capacity of a species to establish, spread, and increase in abundance in a new community or system. Here, invasive and invasiveness do not imply pest impact, only degree of success [26], but highly invasive species have been linked to impacts [68].

Naturalized: an exotic species that establishes self-sustaining populations within natural habitats to become integrated with native community members.

Preadaptation: a trait that now enhances fitness and was built by natural selection for the same function but in a different evolutionary context [76].

Propagule pressure: the number of propagules (e.g., seeds, spores) arriving at a specified location.

Provenance: place of origin and associated ecological–evolutionary history.



Trends in Ecology & Evolution

Figure 1. Community Assembly Theory Applied to Biological Invasions. According to community assembly theory, the composition and relative abundance of species within a community are determined by a series of hierarchical filters that allow or impede the passage of each prospective community member based on its functional traits (each shape represents a species with unique traits; orange indicates exotics and blue natives). Applying these concepts to understand biological invasions requires accounting for initial trait sets within global species pools and how they are filtered by human-facilitated dispersal processes to determine which exotic species traits reach introduced and regional species pools. The exotic and native trait sets in the regional species pools then pass through local intrinsic abiotic and biotic filters to determine the composition and relative abundance of species within the community. The extrinsic processes feeding the regional species pools apply uniquely to exotic species and can cause differences in trait sets between exotic and native species within regional species pools that can introduce provenance biases despite intrinsic processes acting on species traits without regard to species' origins (here, trait similarity is spatially correlated, with more ruderal traits to the right grading toward more competitive traits to the left).

individual fitness (*sensu* [38]). Importantly, any particular filter can differ in nature and strength among communities as a function of the abiotic and biotic context of each system [43]; that is, community assembly is a context-dependent, community-specific process. Of course, multiple filters are generally at work in any system and can act on the same or different functional traits of each species in hierarchical and interactive ways [44]. Despite this complexity, a manageable subset of key traits and filters can have substantial power to explain community structuring [6,45]. For example, while the theoretical range of plant traits that could be expressed is extensive, ecological tradeoffs greatly constrain realized trait distributions [46]. Such context-dependent tradeoff limitations have allowed global variation in tree community structuring to be explained by a few key functional traits and their interplay with competition and environmental context [47].

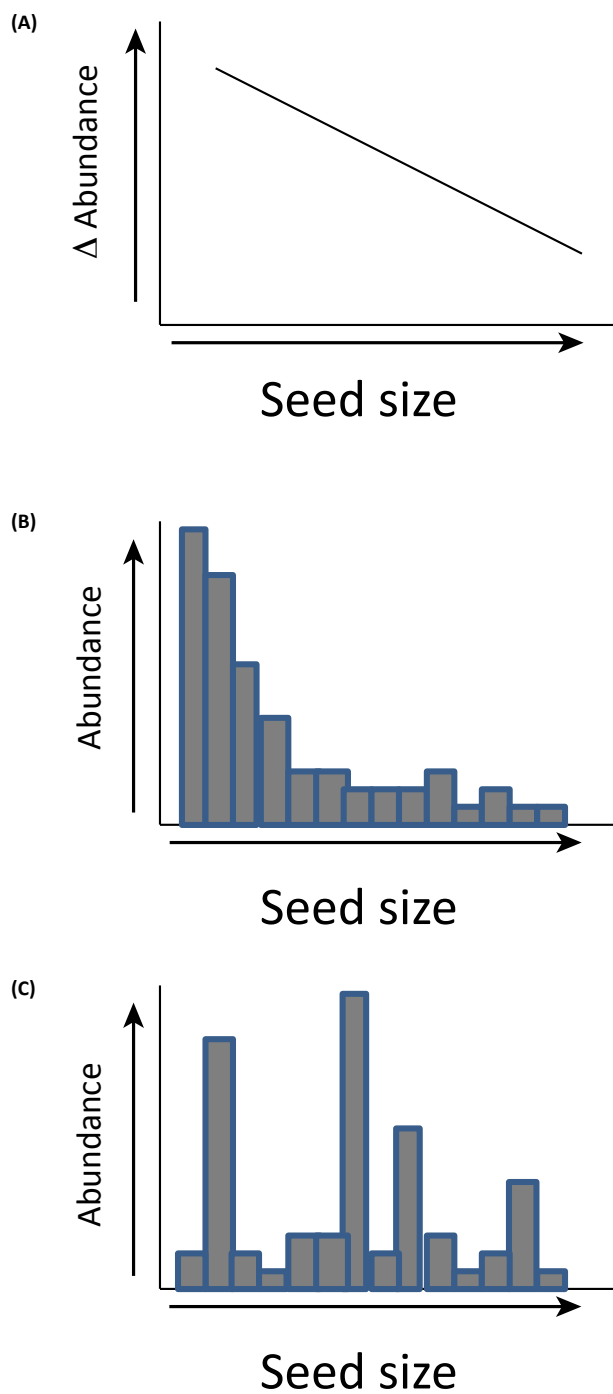
Empirically, the relative importance of a filter can be evaluated by comparing species' responses to that particular filter with their relative abundances in the community [47,48] (Figure 2). The importance of a filter should be indicated by the proportion of the community structure that it is able to explain, with additional filters explaining increasing amounts of variation up to the point where residual variance can be attributable to stochastic effects. For example, if seed predation is a primary factor affecting plant community structure in a particular system, as has been shown for arid plant communities in the southwestern USA [49,50], the relationship between seed traits and species' sensitivity to that filter should explain substantial variation in the composition and relative abundance of species within the community (Figure 2). In more mesic systems, soil feedbacks can be an important filter [45], with additional filters increasing the capacity to describe overall community structure. The assembly framework can also incorporate neutral or stochastic processes [39,51,52] and can be applied to any taxon in contexts ranging from natural to highly applied [6,37,38,53].

Previous authors have recognized the value of applying concepts from assembly theory to biological invasions (e.g., [23,25,54–58]), and several invasion frameworks incorporate elements of community assembly theory [24,26,33], but assembly theory has not been fully integrated into invasion ecology [23]. Moyle and Light [23,25] applied general rules derived from assembly theory to explain invasion outcomes across disparate aquatic systems and determined that invasion outcomes were too idiosyncratic for such rules to be useful. Their conclusions underscore the fact that context dependence is a key obstacle to the development of global rules for explaining invasion outcomes. We propose that community assembly theory can be applied in a manner that accounts for context dependence while also incorporating the other key invasion elements identified above if it is fully integrated into invasion ecology. Accomplishing this requires that: (i) assembly rules be defined at the community scale to address the community-specific nature of invasions; and (ii) higher-level biogeographic assembly processes that determine provenance effects are also accounted for (Figure 1).

Community Assembly Theory as a Framework for Biological Invasions

The community assembly framework can be adapted to address exotic species invasions by integrating pertinent biogeographic and anthropogenic factors linked to human-facilitated invasions (Figure 1). In general applications of assembly theory, the global species pool and associated dispersal filter are ignored because natural global-scale dispersal is rare. However, global species pools must be accounted for to address exotic species invasions, as they determine the gamut of trait sets available for introduction. Importantly, trait sets within these exotic donor pools can differ substantively from those in native species pools given their disparate ecological and evolutionary histories [59–62]. Of course, exotic species arrive via human means rather than natural dispersal, so a translocation filter must be incorporated to account for anthropogenic introduction pathways that can filter for specific traits [63]. In combination, the global species pool and translocation filter determine the makeup of the exotic trait sets entering introduced species pools, defining the raw materials that supply regional species pools. Because community assembly processes act on species traits, differences in trait distributions between exotic and native species pools can generate provenance biases in the final community structure. Additionally, provenance effects can arise via anthropogenic influences on dispersal processes that can increase exotic **propagule pressure** through human transport and agricultural subsidies [21,31,63,64]. Such elevated propagule pressure can allow exotics to numerically overcome filter limitations at multiple levels of assembly.

To fully understand biogeographic invasions, extrinsic and intrinsic processes must be integrated and differentiated (Figure 1). The extrinsic processes associated with the global species



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Figure 2. Mapping Individual Filter Effects onto Community Composition and Relative Abundance. (A) Demonstrates a strong negative effect of the seed predation filter on plant species abundance as a function of seed size. (B) Depicts a community where this filter plays a dominant role in structuring the final community, explaining much of the variation in species relative abundance. (C) Depicts a community where the same seed predation filter fails to explain community structure, suggesting that other filtering processes such as abiotic or competitive effects on seedling survival override or mask seed predation effects.

pool and translocation and human-facilitated dispersal filters apply specifically to exotic species and can generate provenance effects that influence intrinsic filters by biasing exotic trait sets and/or determining the numbers of incoming exotic propagules. By contrast, intrinsic processes apply to native and exotic species alike as a function of their traits. Importantly, some exotic traits can interact with and redefine intrinsic filtering processes [65]. By accounting for the unique roles of extrinsic and intrinsic processes, we can delineate the boundaries between natural and human-facilitated invasions to establish which concepts apply to all organisms and which apply uniquely to exotic species, thereby resolving the provenance debate.

In the context of this framework, understanding the full range of invasion outcomes and linking specific outcomes to appropriate invasion hypotheses requires evaluation of how community-specific filters influence invasions. Because invasion is more akin to community reassembly than nascent assembly (see ‘reassembly rules’ [6]), this can be accomplished by defining the ‘rules’ or parameters structuring the native community as a benchmark or null expectation against which invasion outcomes can be evaluated. Empirically, this involves manipulating community filters to define *in situ* rules by evaluating how traits of native species influence their response to the filter and then evaluating exotics against this standard. Assuming that a particular filter is ecologically important (Figure 2), it should be possible to evaluate invasion outcomes within this framework (Box 1 and 2). Based on recent empirical work [71–73], we might expect that: (i) a few exotics would reside above the trait–abundance line (see Figure 1 in Box 1), indicating that they are gaining advantage relative to the natives by ‘breaking the rules’; (ii) many exotics might fall along the line, indicating that they are ‘behaving like the natives’ and becoming **naturalized** in accordance with filter rules; and (iii) a subset of exotics might fall below the line, indicating that they are disproportionately penalized by the rules. Evaluating how exotics interact with community filters relative to natives in this way provides a context-dependent metric for linking exotic species’ traits with their invasiveness based on

Box 1. Empirical Applications of Community Assembly Theory: Individual Filters

Community assembly theory provides a conceptual framework against which empirical data can be evaluated to elucidate invasion outcomes (Figure 1). It also provides a recipe for invasion research. Evaluating how the functional traits of native species influence their fitness responses to important community filters can define local assembly rules to provide a context-specific metric for evaluating how exotic traits influence invasiveness, when provenance effects might be at work, and which invasion hypotheses might explain specific invasion outcomes. We demonstrate these ideas using data from published studies evaluating the effects of seed predation on plant recruitment.

In grasslands of Montana, USA, rodent seed predation is a strong filter, with increasing seed size linked to reduced native plant recruitment [55,66] (Figure II). While the abundance of most exotics could be predicted from this rule, follow-up studies demonstrate that the exotic outlier *Tragopogon dubius* experienced strong biotic resistance that greatly limited its abundance at the community level [67] and hence its impact on native plants [68]. By contrast, follow-up studies on *Centaurea stoebe*, an exotic that evaded suppressive filter effects, indicated that it achieved high abundance at the community level, which facilitated impacts on native plants [68]. Laboratory studies of *C. stoebe* suggested that novel seed chemical defenses might facilitate its release from natural enemies [55]. Parallel studies suggest that *Bromus tectorum*, another notorious western North American weed [69], also experiences release from seed predators, which facilitates higher recruitment relative to native species in the Palouse Prairie of Washington [70] and the Great Basin of Utah (J.E. Lucero, PhD thesis, University of Montana, 2017).

In central Argentina, ant seed predation suppressed recruitment of smaller over larger seeded natives [56] (Figure III). While most of the exotics followed the seed size rule governing natives, *Carduus nutans* was overly suppressed for its size – a result linked to elaiosomes on its seeds. In its native range, elaiosomes facilitate dispersal by carnivorous ants, which consume the elaiosomes and discard the seeds. In the introduced region, granivorous ants eagerly consume both elaiosomes and seeds, demonstrating how an evolutionary adaptation can be maladaptive in the wrong ecological context. Interestingly, most exotics in this study were smaller seeded than the natives (Figure III). This provenance bias in seed size strongly suggests the influence of higher-level extrinsic processes associated with exotic donor pools, translocation filters, or human-facilitated dispersal [56].

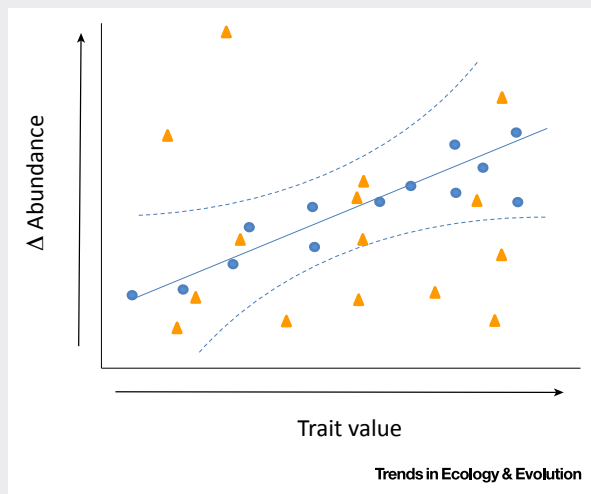


Figure I. Defining Local Assembly Rules for Evaluation of Exotic Species Success. This hypothetical example illustrates how quantifying responses of native species (blue circles) to an intrinsic filter (determined from manipulating the filter and measuring effects on native abundance) in relation to species traits can define assembly rules that can then be used to evaluate how exotic species' traits (orange triangles) relate to their success or invasiveness in recipient communities. In this scenario, the filter has a strong influence on the abundance of native species as a function of trait values (e.g., a quantitative trait metric such as seed size), as defined by the blue trait–abundance line. For exotics falling within the confidence interval (CI) (blue broken lines), abundance is reasonably predicted by how their traits interact with the filter, similar to the natives. For exotics residing outside the CI, the trait does not predict abundance as expected based on this null model, suggesting that novel interactions are at work.

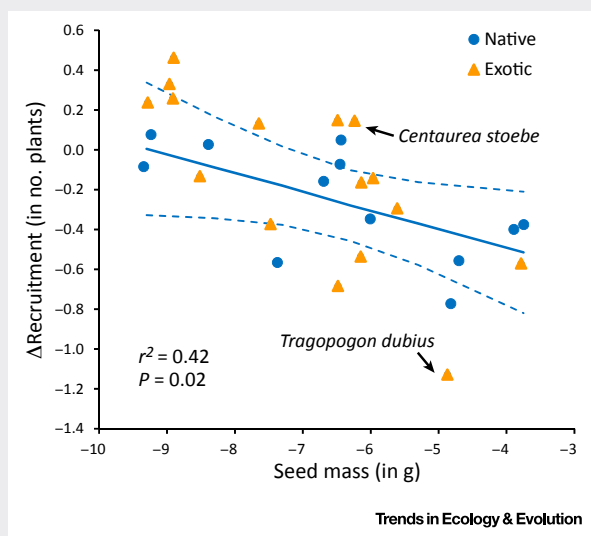


Figure II. Defining Rodent Seed Predation Filter Effects on Plant Recruitment via Seed Size in Montana, USA. Species' responses to seed predation were measured as their change in recruitment outside versus inside rodent exclusion plots (diminishing numbers indicate greater suppressive effects) using data from [66] pooled across disturbance treatments. The trait–abundance line (blue line) was defined as the relationship between the response of native species (blue circles) to seed predation and seed size, based on regression. Significant deviations from this line, as defined by the 99% confidence interval (broken lines), indicate outliers, including several exotic species (orange triangles) whose recruitment is not predicted by the rules of the seed predation filter.

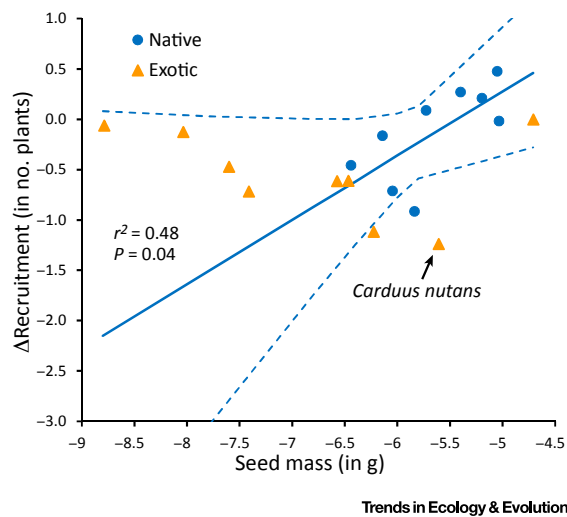


Figure III. Defining Ant Seed Predation Filter Effects on Plant Recruitment via Seed Size in Central Argentina. Species' responses to seed predation were measured as their change in recruitment between ant exclusion and ant access treatments (diminishing numbers indicate greater suppressive effects) using data from [56]. Methods and symbols follow Figure II.

community-specific abiotic and biotic conditions (Box 1). This approach also highlights when provenance might influence invasion outcomes and indicates which invasion hypotheses provide plausible explanations for specific invasion outcomes.

For those exotics fitting the trait–abundance line, their response is predicted by their functional traits similar to the natives, indicating that provenance has negligible influence over these outcomes. The finding that traits can directly predict exotic species abundance according to local community rules, even for a subset of species, represents an advance for invasion ecology. By contrast, deviations from the line indicate potentially important roles of provenance in determining exotic abundance. Deviant exotics are presumably experiencing novel interactions in the recipient community linked to their disparate ecological–evolutionary histories. Such deviant outcomes would invoke specific invasion hypotheses indicated by species' responses to the filter. For example, if the filter represents natural enemy effects and the exotic attains higher abundance than predicted by its trait value, the enemy release hypothesis [11] might explain the success of this particular exotic relative to natives. By contrast, exotics falling below the trait–abundance line might invoke the biotic resistance hypothesis [11]. Notably, some exotics can achieve abnormally high abundance relative to native species due to provenance effects (see Figure I in Box 1, upper left exotic), while others can achieve community dominance without violating community rules simply by exhibiting trait values that confer high abundance given local processes (see Figure I in Box 1, upper right exotic). Importantly, such high abundance can facilitate impacts on natives [68] via either mechanism.

For those deviant exotics whose trait values do not explain their relative abundance in the community, the question is what factors do explain their abundance? Deviations from a specific trait–abundance line imply that other traits or processes are acting to override or exacerbate filter effects. The nature of the filter should provide hints to such novel interactions. Assuming that our natural enemy filter represents herbivory effects on plant abundance as a function of

leaf carbon-to-nitrogen ratios, exotics residing above this line might have novel chemical or physical defense traits relative to native plants. From a proximate standpoint, identifying the specific traits underlying such novel interactions would be sufficient to understand the success of these exotics relative to the natives. However, from an ultimate standpoint comparative

Box 2. Empirical Applications of Community Assembly Theory: Multiple Filters and Mapping Filter Effects

The importance of a local filter is indicated by how closely species' responses to the filter map to community structure. John Klironomos [45] demonstrated the importance of plant–soil feedbacks as a biotic filter when he related feedback responses to plant abundance in a Canadian old-field system. While traits underlying the filter responses were not examined, we used data from this study to evaluate how well filter effects predict the abundance or success of each exotic species in the community (Figure 1). Linear regression indicated that filter responses explained 66% of the variation in native species abundance, confirming the importance of this filter in determining community structure. Applying the community assembly framework to these data provides additional insights beyond the original conclusion from this study. It demonstrates that the abundance of many but not all exotic species was predicted by their feedback responses in accordance with the local assembly rule as defined by the natives. However, the four most abundant exotics performed substantially better than expected based on their feedback responses alone, suggesting that other filters or processes must be considered to fully understand the success of these (and other) outlying species.

In many cases, multiple filters will be required to explain community outcomes. Building on the example in Box 1 (Figure II), we examine the interplay between two filters by evaluating how disruption of the plant competition filter via a disturbance treatment (plants removed vs intact) altered the effects of rodent seed predation on plant recruitment [66]. In the presence of plant competition, larger-seeded natives were more impacted by seed predation than smaller-seeded natives, with most exotics conforming to this local assembly rule (Figure II A). However, disrupting the competition filter altered the response of many exotics to the seed predation filter, causing them to deviate from the native baseline (Figure II B). Overall, exotics benefited more than natives from the removal of competition [66], but smaller-seeded exotics benefited most from these combined effects because they were relatively immune to seed predation. However, the advantage of exotics over natives following disturbance cannot be fully explained by these local assembly rules and was further attributed to biases in exotic donor pools toward species bearing more ruderal traits [66] (see also [78]).

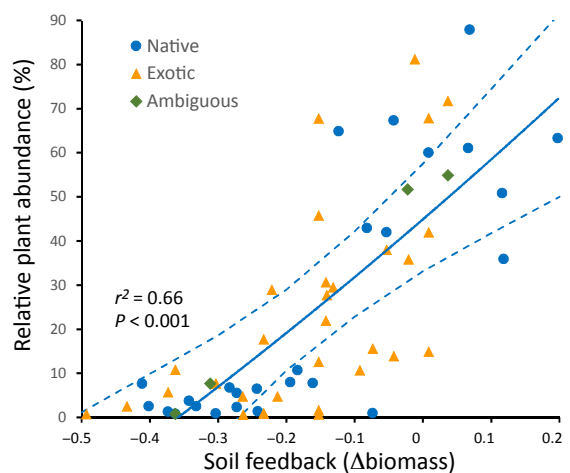


Figure 1. Evaluating the Potential Influence of a Soil Feedback Filter on Exotic Plant Success in Old-Field Systems of Southeastern Canada. The relative abundance of native species in the community (blue circles) correlated well with their mean soil feedback responses based on linear regression (blue line) (data extracted from [45], see Figure 3). The abundance of many exotic species (orange triangles) was predicted by this assembly rule, but several deviated significantly based on the 99% confidence interval (broken lines), indicating that additional filters or processes are likely to influence exotic success, particularly for the more invasive plants. Origin was ambiguous for some species

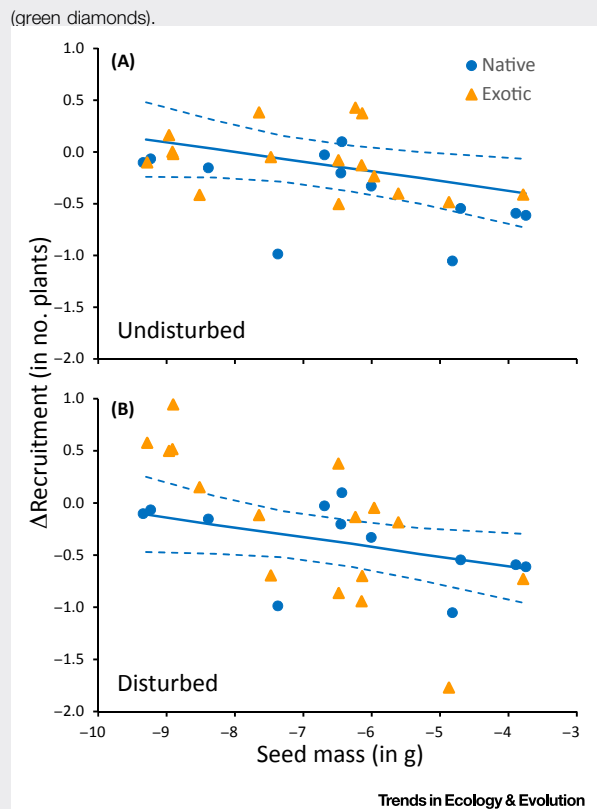


Figure II. Evaluating the Effect of Disturbance (Disruption of the Competition Filter) on the Seed Predation Filter for Native (Blue Circles) and Exotic (Orange Triangles) Plant Species. Species' responses to seed predation were measured as the change in recruitment outside versus inside rodent exclusion treatments, in undisturbed and disturbed plots, respectively (diminishing numbers indicate greater suppressive effects), using data underlying [66]. Trait–abundance lines (blue) were defined by relationships between native species' responses and seed size determined via a generalized linear model that included disturbance. In the absence of disturbance (A), larger-seeded natives were more impacted by seed predation than smaller-seeded species ($F_{1,11} = 7.2$, $P = 0.02$), with most exotic species falling within the 99% confidence interval (CI) (broken lines). Disturbance (B) generally intensified the rodent effect on native species ($F_{1,11} = 6.4$, $P = 0.03$). Although disturbance did not alter the slope of the trait–abundance line for native species (seed size $\times$ disturbance from full model: $F_{1,10} = 0.1$, $P = 0.73$), smaller-seeded exotics in particular gained advantage over natives, residing above the CI.

biogeographic studies would be required to establish the fitness value of the trait in the native relative to the introduced range to determine whether an exotic has experienced a biogeographic advantage [72] and/or whether associated traits were preadapted for their function in the new system, as is often inferred (e.g., [74,75]), or exapted from other purposes (*sensu* [76]), as can apply to some novel weapons [12]. Whether the underlying cause is **preadaptation** or **exaptation**, this framework suggests that the paradox of introduced species outperforming locally adapted natives can be attributable to novel interactions between exotic traits and local community processes.

Community Assembly Theory Explains Invasibility More Fully than Fluctuating Resources

Invasibility is a fundamental metric of community stability. The fluctuating resource hypothesis (FRH) postulates that community invasibility is determined by fluctuations in resource availability

arising from changes in extrinsic resource inputs or disruptions of intrinsic controls over resource uptake such as those generated from disturbances [13]. However, as noted by the FRH's authors, these processes act on species traits independent of origins, so they should not generate provenance-biased outcomes. Hence, while the FRH has greatly advanced our understanding of invasibility, it cannot explain why disturbances commonly favor exotic over native species [14,15]. In the context of community assembly theory, invasibility is an emergent community property arising from the collective effect of all intrinsic filters or processes (as influenced by disturbances or perturbations) on the establishment and success of new species, conditioned by all extrinsic processes and inputs. Whereas the FRH emphasizes one important filter and process – competition and its effects on resource availability – the community assembly approach can incorporate the effects of all filters and processes on invasibility. For example, the community assembly framework can integrate the filtering effects of pathogens, predation, and herbivory, which can act independently of and interactively with competition and resource availability to influence invasion outcomes (Box 2) [66,77]. Moreover, as discussed above, by incorporating extrinsic processes the community assembly framework can account for the effects that global species pools and translocation filters have on intrinsic invasion processes, to explain provenance-biased outcomes [78]. This comprehensiveness and adaptability of community assembly theory facilitates the integration of anthropogenic influences like climate change, nutrification, and altered disturbance regimes (incorporated as changes in filter effects driven by the specific process changes) as well as mainstream ecological concepts like niche–fitness tradeoffs [79] into invasion ecology.

Concluding Remarks

The framework we propose fully integrates community assembly theory with invasion ecology for the first time [23]. Merging these fields delineates the overlap zones and boundaries between invasion ecology as a general science and invasion ecology as a subdiscipline focused on anthropogenic invasions to resolve the invasion paradox and the provenance debate by demonstrating how provenance conditionally influences invasion outcomes. The novelty of this approach resides in the evaluation of exotic traits relative to those of natives in the context of the intrinsic filters that structure communities (conditionality) while accounting for extrinsic anthropogenic assembly processes that uniquely influence exotics. While this framework focuses on community-scale assembly rules, we anticipate that repeating this approach across communities will reveal more generalizable global assembly rules. Our empirical examination of this framework shows promise (Box 1 and 2). We hope that broader testing will vet these ideas and stimulate further advances (see Outstanding Questions).

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Outstanding Questions

To what extent do exotic trait sets arriving in introduced species pools influence invasion outcomes and how are they affected by source pools and filter processes? What relative influence do (i) biogeographic differences in global species pools, (ii) translocation filters acting on traits in transit, and (iii) processes associated with the acquisition of species from donor pools for transit have on the final trait sets arriving in the introduced species pools?

Can we differentiate between anthropogenic and natural sources of propagule pressure sufficiently to understand the relative importance of inherent species traits versus human influences on propagule inputs linked to invasion outcomes?

How many and which community filters are necessary to determine community structure and does the importance of different filters and filter combinations vary predictably over ecological gradients?

To what extent does novelty matter? That is, to what extent do problematic pest species arise from invaders exhibiting novel interactions with local filters versus invaders simply exhibiting high values of traits that garner their success according to local filter rules?

To what extent is community invasibility affected by local filters other than competition and how are those filters affected by perturbations?

Can the community assembly framework be used to develop more general predictive assembly rules for biological invasions? By linking specific invasion outcomes to explicit causal hypotheses, can we begin to build evidence that cumulatively supports or negates specific invasion hypotheses like enemy release, novel weapons, etc.?

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