

Annual Review of Plant Biology

Why Are Invasive Plants Successful?

Margherita Gioria,¹ Philip E. Hulme,²
David M. Richardson,^{1,3} and Petr Pyšek^{1,4}

¹Department of Invasion Ecology, Institute of Botany, Czech Academy of Sciences, Průhonice, Czech Republic; email: margherita.gioria@ibot.cas.cz, pysek@ibot.cas.cz

²Bioprotection Aotearoa, Lincoln University, Lincoln, New Zealand; email: philip.hulme@lincoln.ac.nz

³Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Stellenbosch, South Africa; email: rich@sun.ac.za

⁴Department of Ecology, Faculty of Science, Charles University, Prague, Czech Republic

Annu. Rev. Plant Biol. 2023. 74:635–70

First published as a Review in Advance on February 7, 2023

The *Annual Review of Plant Biology* is online at plant.annualreviews.org

<https://doi.org/10.1146/annurev-arplant-070522-071021>

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Keywords

alien plants, non-native plants, invasive species, biotic interactions, competition, ecosystem invasibility, functional traits, invasiveness

Abstract

Plant invasions, a byproduct of globalization, are increasing worldwide. Because of their ecological and economic impacts, considerable efforts have been made to understand and predict the success of non-native plants. Numerous frameworks, hypotheses, and theories have been advanced to conceptualize the interactions of multiple drivers and context dependence of invasion success with the aim of achieving robust explanations with predictive power. We review these efforts from a community-level perspective rather than a biogeographical one, focusing on terrestrial systems, and explore the roles of intrinsic plant properties in determining species invasiveness, as well as the effects of biotic and abiotic conditions in mediating ecosystem invasibility (or resistance) and ecological and evolutionary processes. We also consider the fundamental influences of human-induced changes at scales ranging from local to global in triggering, promoting, and sustaining plant invasions and discuss how these changes could alter future invasion trajectories.

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1. INVASIONS BY NON-NATIVE PLANTS

Plant invasions are a global phenomenon associated with human activities and socioeconomic drivers (217). Human activities are important in not only transporting non-native plants beyond their native distribution ranges at unprecedented rates (177, 246) but also promoting range expansion within the introduced ranges, even in protected or highly biodiverse systems (13, 71, 210, 233, 282). Moreover, invasions are mitigated or exacerbated by negative and positive feedback loops resulting from people's movements, behavior, and response to the collection, transport, introduction, and spread of non-native species (251). There is also evidence that new introductions may be expanding faster than past or current invasions (290). This evidence, coupled with global environmental changes that inevitably interfere with biotic interactions in the new ranges, requires a deep understanding of the drivers of the successful establishment and spread of non-native plants to predict and prevent new invasions and manage the current ones (86, 123, 215).

The stages of the invasion process form the so-called introduction-naturalization-invasion continuum (hereafter invasion continuum) (235). Following an introduction, a species must negotiate a series of environmental and reproductive barriers or filters to progress along the different stages of the invasion continuum (13, 17, 233, 235). These barriers can prevent the introduced propagules from establishing viable populations (249). Some species survive only temporarily in the new region (casual species); others establish self-sustaining populations (naturalized species); and some of these naturalized species spread rapidly, become widespread, become locally abundant, and/or occupy a variety of habitats (invasive species) (13, 78, 194, 234). Consequently, only a small proportion of non-native species become established and even fewer become invasive (13, 235, 289). Rapid population growth, range expansion, and increase in local dominance are reported for many invasive plants, but many non-native species experience long lag phases before they start to proliferate and spread (4, 43, 100, 148, 195).

In this paper, the term invasion success refers to plant species that progress along the invasion continuum and pass through consecutive stages to become invasive. The probability of a species overcoming these ecological barriers and progressing along the invasion continuum has been typically examined as a function of (*a*) intrinsic factors, that is, inherent plant properties or functional traits that determine its invasiveness (163, 218, 236); (*b*) extrinsic ecological and evolutionary processes associated with the characteristics of the recipient ecosystems that determine

Range expansion:

a process whereby a species (native or non-native) spreads into new areas adjacent to its current distribution, with or without human intervention

Introduction-naturalization-invasion continuum (invasion continuum):

a conceptualization of the progression of stages and phases in the status of an organism introduced to a new environment

Lag phase:

the time between the arrival of a species in a new area and the onset of a rapid or exponential population growth and range expansion

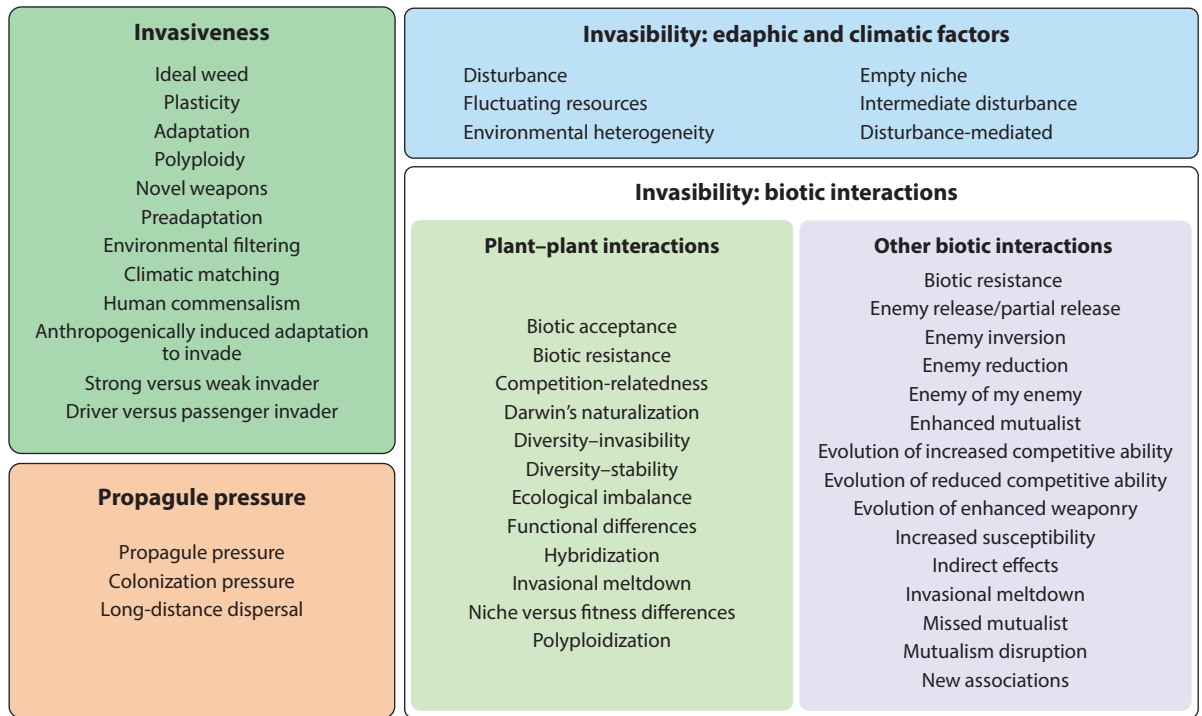


Figure 1

Hypotheses presented in this review that have been used in the literature to evaluate the invasiveness of non-native plants or the invasibility of native ecosystems. Hypotheses formulated on the importance of biotic interactions on invasion success are distinguished depending on whether they refer to plant–plant interactions or other biotic interactions. Propagule pressure acts as a bias in analyses aimed at determining the role of species traits in promoting invasiveness and the invasibility of the recipient ecosystems by increasing opportunities for successful establishment, hybridization, and long-distance dispersal.

their susceptibility to invasions, that is, invasibility (29, 34, 36, 38, 50, 70, 77, 163, 180); and (c) introduction effort, termed propagule pressure, defined as the number and frequency of propagules (i.e., any reproductive structure of a plant) introduced into a system (17, 28, 36, 160, 163, 249). The associated term colonization pressure refers to the number of species introduced (160).

We build on the review by Richardson & Pyšek (233) to discuss progress in understanding how species properties at different stages of the invasion continuum and the characteristics of the recipient ecosystems influence ecological and evolutionary processes, leading to successful invasions by terrestrial plants, and why some species become invasive in some ecosystems while others fail. Our focus is on ecological processes occurring at the local (community) scale. We refer to the most influential hypotheses proposed to explain invasion success (62, 211) (**Figure 1**) and theories that attempt to unify some of these hypotheses (**Table 1**). We describe how levels of consensus for many paradigms in invasion ecology have changed over time as evidence has accumulated, new or more rigorous hypotheses have been tested, and the potential effects of multiple (rather than individual) drivers have been investigated (65, 215, 220, 286). The inherent context dependence of invasions (30, 215) demands the consideration of the joint effects of species traits, environment, and socioeconomic characteristics to explain and predict plant naturalizations and invasions.

Invasion success: the extent to which a non-native species can negotiate barriers and exploit opportunities along the invasion continuum, often expressed by its rapid population increase, local dominance, and rapid range expansion

Table 1 List of theories and frameworks that have been proposed to unify multiple hypotheses on key ecological processes or drivers of successful invasions

Framework	Description of the framework	Key process or drivers	Source
Williamson framework	Invasions as a series of stages: casual, naturalization, and invasion	Non-native species traits; habitat properties; human activities (including propagule pressure)	289
Disturbed Resource-Flux Invasion Matrix (DRIM)	An integrative method classifying habitats in a 16-cell matrix depending on quality of changes in physical and chemical resource flux (relative to historical patterns)	Disturbance	248
Richardson framework	Barriers along the introduction-naturalization-invasion continuum	Geographic, environmental, reproductive, dispersal, and environmental barriers	235
State factor model (quantitative)	State factor model that incorporates five broadly defined state factors	Propagule pressure; properties of the introduced habitat; invading species (or genotype) autecology; properties of the source habitat; residence time	8
Vacant niches	Invasion success attributed to vacant niches that become available under environmental changes	Resident species traits; invasive species traits; environmental conditions	180
PAB framework	Invasion success resulting from propagule pressure (P), abiotic characteristics (A), and biotic characteristics (B), with the additional influence of humans (H) on P, A, and B	Propagule pressure; habitat properties; human activities	28
Niche versus fitness differences	Coexistence and competitive exclusion, which vary along two axes: niche differences versus fitness differences	Functional differences between native and non-native species	167
Unified framework for biological invasions	Stages separated by barriers	Geographic, cultivation, survival, reproductive, dispersal, and environmental barriers	13
Expanded framework of plant invasion ecology	Hierarchical framework with three contributing processes	Non-native species traits; system context; habitat characteristics	70
Invasion triangle	Invasion success as the result of three processes located at the sides of the invasion triangle	Potential invader attributes; biotic characteristics; environmental conditions; external influences (climate change and land-use change)	207
Invasion syndromes	Four invasion syndromes relating invader attributes to the biotic characteristics and environmental conditions of invaded sites	Invader attributes (competitive ability, niche construction, phenotypic plasticity, and phenological niche separation); biotic characteristics (biodiversity and enemies); environmental conditions (resource abundance and fluctuation)	208
Quantifying invasiveness	Mathematical framework aiming to quantify the invasiveness of species along two axes: (a) native and non-native differences in performance within a region; (b) intraspecific differences in the native and non-native range	Attributes of non-native species in the native and non-native ranges; comparison with native species	38

(Continued)

Table 1 (Continued)

Framework	Description of the framework	Key process or drivers	Source
Ecological networks	Models the structural stability and invasibility of the recipient ecological networks	Species invasiveness (invasion fitness); ecosystem invasibility (assembly saturation)	119
Invasion factor framework	Three components of the invasion process, which are influenced by three factors	Components of the invasion process: rapid population increase, established local dominance, and rapid range expansion; three factors influencing the invasion process: ecosystem resistance, invader fitness, and climate dynamics	299
Conceptual map of hypothesis	Conceptual map grouping 39 hypotheses on biological invasions into 5 clusters and linking individual hypotheses to each other	Darwin's, trait, biotic resistance, propagule pressure, and resource availability clusters	62
Macroecological Framework for Invasive Aliens (MAFIA)	Invasions as a function of non-native species traits, location characteristics, and factors related to introduction events	Non-native species traits; habitat characteristics and climate; pathways of introduction; socioeconomic context; propagule pressure; residence time	215

2. SPECIES INVASIVENESS

2.1. The Importance of Species Traits Along the Invasion Continuum

The search for inherent biological properties—functional traits and their plasticity—that make plants successful invaders has received much attention (36, 220, 222, 225, 226, 234, 277), dating back to the identification of the characteristics of the ideal weed typically associated with human activities (7) (**Figure 1**). An underlying assumption of trait-based approaches is that invasion success is associated with one or more functional traits of non-native species (38) and depends on how these traits make a species preadapted to the biotic and abiotic characteristics of the recipient ecosystems (18, 73).

Invasive species have specific combinations of traits that promote establishment, population increase, and range expansion and that are, in some instances, useful to outcompete resident species in the non-native ranges (57). Functional traits vary in their importance along the invasion continuum (54, 185, 219, 235). Some traits confer advantages for establishment; others may become important during the invasion stage because the barriers and filters characterizing these phases differ (235). A well-developed theoretical framework describes how environmental factors mediate naturalization (13, 18, 28, 221, 233, 234). The realized ecological niche of a species is a function of the environmental conditions a species can tolerate and requires for survival and reproduction (i.e., its fundamental niche) and of biotic interaction with other species (competitors, natural enemies, and mutualists). Environmental filtering has long been regarded as a major driver of the successful naturalization of non-native plants (18) (see Section 3.1). A non-native species is expected to become naturalized if its fundamental ecological niche matches the conditions in the new range (18, 53). This correspondence depends on preadaptation (275), including climatic preadaptation or climatic matching (83, 262) or preintroduction selection (17, 37), and varies with the characteristics of the recipient ecosystems (13, 18, 85, 86, 234, 261). A recent synthesis of empirical evidence indicates that invasive plants tend to prefer climates similar to those they encounter in their native range and that there is very limited climatic niche expansion between native and introduced ranges, with non-native species occupying similar niches as natives in the environmental space (158). However, even if its ecological requirements are met, a non-native species encounters

Functional traits:

morphological, biochemical, physiological, structural, phenological, or behavioral characteristics of individual plants (phenotypes) that determine their response to the environment

Invasiveness:

the biological properties of a species that determine its capacity to be invasive after its introduction into new ranges

Invasibility:

the properties of a community, habitat, or ecosystem that determine its vulnerability to invasion by non-native species

Propagule pressure:

a concept encompassing variation in the quantity, quality, composition, and rate of supply of non-native propagules in an area

Ecological niche: the range of resources and conditions needed to allow a species to maintain a viable population

Competition:

a negative interaction between individuals associated with a requirement for shared limited resources, potentially reducing the fitness of individuals or populations

a degree of biotic resistance associated with competition from native species (61, 155), new natural enemies (200), and/or the absence of its mutualists (179). A criticism of invoking environmental filtering as a mechanism for selecting against certain non-native species is that other mechanisms such as competition can generate similar, indistinguishable patterns (20).

Because founder population sizes are usually small due to limited propagule input (160) or survival and are prone to stochastic extinction (249), reproductive traits are key to overcoming barriers to establishment (88, 185, 186, 223, 234, 275). High seed production and/or a capacity for extensive vegetative propagation and growth can be useful at multiple stages of the invasion continuum, and many invasive plants have such traits (126, 186, 222, 277). Comparative studies suggest that species- or individual-level traits associated with regeneration, such as seed mass (185, 233), self-compatibility, and autofertility (223), facilitate establishment in the introduced ranges. Also, producing seeds that persist in the soil over multiple seasons greatly increases the probability of naturalization (88, 220) and the geographic extent of naturalization (88), especially in annual and perennial herbs. This has important consequences for the persistence and resilience of introduced populations, allowing seeds to persist in the soil even during unfavorable conditions, hence increasing opportunities for successful seedling recruitment (88).

A capacity for long-distance dispersal is an important determinant of range expansion rates (150, 186, 295). However, field evidence of long-distance dispersal is often contrasting and difficult to collect (44, 233, 296). Molecular studies have helped to disentangle how the mode of dispersal, admixture among plant lineages resulting from repeated introductions, and plasticity in reproductive strategy mediate plant invasion dynamics (252, 296) and shape the global and regional distributions of non-native species (6, 252). Genetic analyses have also improved our understanding of which genotypes of global invaders colonize and spread in the introduced ranges (3) and how invasion patterns and trajectories respond to climatic change along environmental gradients (44, 159). They have even shown how communities of granivores that disperse the seed in the new range have shaped the population density and distribution of non-native plants such as dandelions (*Taraxacum officinale*) (166).

Naturalization and invasiveness have long been related to superior ability to compete for resources compared to native species (90). Performance traits related to fitness, growth rate, size, biomass allocation, and physiology are regarded as good predictors of invasiveness (53, 150, 233, 277). Many invasive species have preadaptations that are useful in the early stages of succession (29) and in disturbed habitats (86, 134, 277). However, the presumed importance of rapid nutrient acquisition, growth, and reproduction in determining invasion success may be mainly due to ruderal species colonizing nutrient-rich, disturbed habitats (183). The high proportion of invasive species possessing these performance traits might also reflect an introduction bias; the capacity for trait plasticity contributes to invasiveness and favors introduction. In other words, species with those traits might have been preferentially selected by humans for intentional introduction (18, 33). This intersection might partly explain why non-native species that are introduced intentionally are more likely to become invasive than those introduced accidentally (33, 172).

Functional traits influence not only the strategies that plants adopt to acquire and use resources but also their ability to alter resources available to other plants. An example is the ability to fix nitrogen, a trait often associated with invasiveness and shared by many invasive woody and herbaceous plants, such as *Gunnera tinctoria*, *Morella faya*, and *Ulex europaeus* (27, 117, 129). Invasive species that possess this trait can alter nitrogen cycling and availability by changing nitrification rates and creating positive feedback that may favor the persistence of the invader (59, 298) at the expense of native species adapted to low-nutrient conditions (79). The magnitude of such feedback depends on interspecific interactions (153). These changes, and, more generally, biogeochemical changes associated with differences in rates in decomposition or nitrogen release between native

and non-native species (59), may also facilitate secondary invasions by other non-native species that take advantage of a high soil nitrogen availability (82, 117).

For some species, invasion success relates to their ability to produce secondary metabolites (i.e., allelopathy) that are evolutionarily novel in their introduced ranges and can inhibit neighboring native plants directly or indirectly by disrupting beneficial mutualisms (i.e., the novel weapon hypothesis) (23, 271). Allelopathic substances are commonly produced by invasive plants (132), although empirical evidence both supports and refutes this hypothesis (191). The full ecological, evolutionary, and coevolutionary implications of allelopathic interactions between non-native and native plants remain unclear (271, 300). Increases in the production of allelochemicals in response to intense resource competition could confer a competitive advantage over natives (300), and the production of allelochemicals often has greater effects on native than non-native species (271, 303). Whether allelopathic ability can evolve in the introduced ranges (i.e., the evolution of increased weaponry hypothesis) (96) remains largely unknown, and we know of no evidence that supports this hypothesis (96, 191). Moreover, the production of allelochemicals is influenced by the amount and quality of available resources (40), closely tying any impacts of allelopathy on native communities to resource dynamics in recipient ecosystems. A recent synthesis showed that native species are more strongly inhibited by naturalized species than by other native species, while naturalized species are less likely to suppress other naturalized species than the natives, even if they often do not share a coevolutionary history with other naturalized non-native species (303). The fact that the negative effects of allelopathy are greater with increasing phylogenetic distance suggests that allelopathy could contribute to the dominance of invaders that are distantly related to non-native species or their coexistence with closely related non-native species (303).

Failure to recognize the different contributions of individual functional traits along the invasion continuum has led to contradictory findings on their importance in mediating invasion success (54), and some traits have been reported to contribute in opposing ways to naturalization and invasion. For example, large seeds are associated with naturalization, while small-seeded species are more likely to be invasive (185, 219). This contrast emerges because a larger seed mass may provide a species with a short-term competitive advantage over small-seeded species at the phase of seedling recruitment (181), but small seeds increase opportunities for dispersal and range expansion over space and time (88). Overall, there is limited scope for meaningful extrapolation of such insights across taxa; for example, insights gleaned from studies of pine trees are likely irrelevant for daisies or orchids.

Several factors hamper our ability to predict invasion success from species traits alone. Propagule pressure and residence time, which is a component of propagule pressure because the number of propagules introduced into the community usually accumulates with the time since introduction, affect the probability of a species becoming invasive (13, 36, 50, 182, 215) (see Section 3.3). These factors often override species traits in promoting successful naturalization or invasions (219, 220). A longer residence time also increases the probability of the successful spread of viable propagules (78, 219, 226) and opportunities for evolutionary changes that might promote invasiveness. Local dominance in plant communities typically increases with residence time, with positive feedback between aboveground population densities and soil seed densities being observed (92).

There is a taxonomic introduction bias: not all species or higher taxonomic groups have been moved around the globe to the same extent. This means that opportunities to become naturalized and/or invasive have been different for different taxa, which in turn constrains the opportunities for unbiased evaluation of the determinants of invasiveness (172, 193, 222, 233). For many intentional introductions, there is also a bias toward species that are preadapted to the climatic conditions in the introduced ranges and species that grow rapidly (107).

Allelopathy:

a biological phenomenon whereby an organism produces biochemicals that negatively influence the germination, survival, and reproduction of other organisms

Residence time:

the time since the introduction of a species into a region, which can be viewed as a component of propagule pressure

Phenotypic

plasticity: the ability of a particular genotype to express a range of phenotypes in different environments

It is also important to note that functional traits also have indirect effects. For instance, functional traits influence the naturalization of Central European species in North America through their effect on the number of habitats occupied in the native range and on cultivation rather than directly on species performance (220). Also, the contribution of traits to predicting naturalization or invasiveness often varies with the spatial and temporal scales at which such effects are assessed and depends on whether phylogenetic relatedness among non-native species is considered (150).

The role of functional traits in determining invasiveness is also mediated by local biotic and abiotic conditions in the introduced range since the ability of a species to progress along the invasion continuum often depends on plastic and/or evolutionary responses to the conditions experienced in introduced ranges (38, 105, 170, 182, 301). Not accounting for variability or changes in key species traits may strongly affect our perception of their role in promoting successful invasions (38) (see Section 2.2).

2.2. The Importance of Phenotypic Plasticity in Promoting Invasiveness

Phenotypic plasticity in ecologically important traits has long been linked with invasion success because the flexibility afforded by plasticity may enhance responses to the biotic and abiotic conditions encountered in the introduced ranges (a concept known as the phenotypic plasticity hypothesis) (228) (**Figure 1**), broadening the ecological niche of a species (42, 188, 228). Moreover, plasticity in traits affecting regeneration and resource use can present an advantage in responding to climatic changes and in promoting range shifts (87) so that species with broad variation in mean trait values may have an enhanced capacity to colonize a wide range of climatic conditions (182). Theoretical frameworks that address the link between plasticity and invasion success (57, 228) postulate that (a) invasive species may maintain high fitness across a broad environmental range due to morphological and physiological plasticity or fitness homeostasis; (b) invasive species may experience greater increases in fitness under favorable environmental conditions than native species do (termed master-of-some) or may be better able to maintain fitness in unfavorable environments (termed jack-of-all-trades); or (c) invasive species may combine these strategies (i.e., jack-and-master), in both stressful and resource-rich environments. Examples from empirical studies include herbs such as dandelion *T. officinale* and *Senecio jacobinae*, which are jack-and-master invaders (182, 259), and *Centaurea maculosa*, a jack-of-all-trades invader (259).

Despite the potential benefits of plasticity in the introduced ranges, empirical evidence is inconclusive (184), as indicated by the contrasting results of meta-analyses. Some found differences in plasticity between invasive and noninvasive species (39, 42), while others reported no major differences (93, 197), although in some comparisons native species were considered noninvasive despite being invasive or potentially invasive elsewhere (273). Moreover, the potential benefits of plasticity may change with the stage of invasion (184). Transplant garden experiments conducted in the native and invaded ranges for two invasive maple tree species (*Acer negundo* and *Acer platanoides*) suggest that plastic effects might be more important during the early stages of colonization than later in the invasion process, when genetic differentiation may contribute more significantly during the spread of established populations (147). In this respect, a biogeographical approach comparing many species (and life forms) from the native and non-native ranges and grown under common conditions, while accounting for maternal effects, has the potential to provide insights into the role of plasticity.

Potential evolutionary changes in plasticity complicate our understanding of how plant populations behave during the invasion process, although this possibility is often overlooked (171). Phenotypic plasticity may be adaptive if the phenotypes produced in response to environmental change result in higher-than-average fitness (72, 228). However, high phenotypic plasticity is not

necessarily correlated with high fitness (46), and the extent to which it may promote successful invasions relative to mean species traits or evolutionary changes remains largely unknown (122, 168; but see 184). Empirical evidence both supports (25, 149) and contradicts (52, 274) the hypothesis that populations of invasive species in introduced ranges have become more plastic than those in native ranges. Huang and colleagues (114) suggested that these inconsistencies may arise from the costs of plasticity, which determine whether the evolution of increased plasticity is advantageous or not. They proposed that the release from natural enemies or any other factor relieving an introduced population from stress may promote the evolution of greater adaptive plasticity by reducing the costs and increasing the benefits of plasticity.

2.3. The Importance of Evolutionary Processes in Driving Invasion Success

Invasion success across broad environmental gradients has often been associated with rapid evolutionary changes in several functional traits in response to new selection regimes experienced in the introduced ranges (37, 55, 105, 146, 149, 170, 182, 242). Since non-native species must overcome different types of barriers along the invasion continuum, it is plausible that each phase of the invasion process leaves traces in the genetic makeup of invading species populations, affecting their ability to succeed in the subsequent phases (37, 146).

Several key evolutionary mechanisms act at different stages of the invasion process (301) (**Figure 1**). Preintroduction history can have important evolutionary effects that may be beneficial in the introduced range (37, 100, 146, 301); such effects include climate preadaptation (146) or human commensalism (86, 116, 134). Hufbauer and colleagues (116) defined the latter scenario as an “anthropogenically induced adaptation to invade,” suggesting that propagules from populations adapted to anthropogenic disturbances in the native range will perform well in similarly disturbed conditions in the introduced range. Moreover, the evolutionary history of a non-native species in the presence of human-induced disturbance is likely to be beneficial under ongoing global changes (37). Yet, adaptation may occur only in the introduced range, and successful invasion may be contingent on the introduction of populations that were especially successful (i.e., the invasive bridgehead effect) (162), although this effect has mainly been tested for animals and not plants.

Allee effects and genetic bottlenecks associated with low initial population size may affect the probability of naturalization of non-native plants (55, 160) and cause stochastic extinctions (249). Multiple introductions may mitigate the effects of severe demographic bottlenecks that reduce the genetic diversity in small founding populations. Many non-native plants have become invasive despite genetic bottlenecks that are expected to result in inbreeding depression, increased fixation of deleterious mutations by genetic drift (i.e., drift load), and reduced evolutionary potential to respond to novel selection pressures (i.e., the genetic paradox of invasions) (55, 65, 243). Avoidance of inbreeding depression and drift load can also be linked to reproductive traits and genetic characteristics, although there is no empirical evidence to explain invasion success where strong genetic depletion, inbreeding depression, and drift load occur (243). It has been suggested that temporary or permanent releases from stressful conditions in the introduced range may mitigate the negative effects of genetic depletion on fitness and that interactions with local environmental conditions may even result in rapid evolutionary changes and contribute to the adaptation of non-native species in the absence of high genetic variation (243).

Selective pressures that may limit the establishment of non-native plants include suboptimal environmental conditions, biotic resistance via competition with native species (75, 90), and acquisition of novel enemies (200), although evolutionary changes associated with the release from specialist natural enemies are also possible (14, 24, 39) (see Section 3.2). At the invasion stage, high

Allee effects:

the positive density dependence that many species experience when population size and/or density is low, primarily due to difficulty in finding mates

Epigenetic: related to the way cells control gene activity without involving alterations in the DNA sequence

densities achieved by many invasive species can facilitate demographic and evolutionary changes that reduce extinction risks in changing environments (37).

Invasion success and invasibility are influenced by opportunities for inter- and intraspecific hybridization among historically isolated populations that generate novel adaptive gene combinations or increase the genetic variation available for adaptive evolution (60, 137). Because abiotic and biotic conditions (and associated stress) vary over time and along the invasion continuum, new allelic combinations and epigenetic changes may contribute to invasion success (187). A growing body of evidence indicates that genetic admixture, hybridization, and polyploidization or increased ploidy are associated with successful naturalization and invasiveness (187, 258, 301). Genome size and polyploidy (the heritable condition of possessing more than two complete sets of chromosomes) are species traits that have been linked to naturalization and invasiveness (141, 198, 256, 258) and play different roles in plant trait expression (176). Autopolyploidy (the acquisition of more than two sets of chromosomes by means of intraspecific genome duplication) and allopolyploidy (the merging of genomes of distinct species through hybridization and subsequent genome duplication) have important ecological and evolutionary consequences for the fate of introduced plant species (258). Polyploidization induces several types of genetic and epigenetic events and alters plant functional traits, producing individuals that can cope with environmental variability and stressful conditions and exploit new niches (187, 240, 254, 258). Polyploid plants are expected to be more successful invaders than diploid plants since polyploidy generates higher fitness during the establishment phase and/or increased potential for subsequent adaptation due to a larger genetic diversity that may contribute to the evolution of invasiveness (112, 237, 238, 258). Polyploids are also less likely to experience inbreeding depression due to the balancing effect of multiple gene copies (238). The combination of higher seedling growth rates and diminished inbreeding depression suggests that polyploids must be more invasive and, therefore, more competitive than diploids (240). Newly formed polyploids have been shown to exhibit rapid range expansion. Examples are *C. maculosa*, in which tetraploids dominate populations in the introduced range (269), and *Solidago canadensis*, in which tetraploids occur only in the introduced ranges and diploids and hexaploids only in the native ranges (121). For *Centaurea stoebe* and *S. inaequidens*, native tetraploids are more competitive than native diploids, which partly explains the invasion success of the preadapted tetraploid genotypes (260). Ploidy level has also been suggested to drive impacts of invasive plants in the introduced ranges, as in the case of *C. stoebe* (257), although the effect might be neutral, as in the case of *Phragmites australis* (216). There is, however, no conclusive evidence that polyploids make better invaders than nonpolyploids (240), possibly because other factors such as propagule pressure may have an overriding influence. It has been suggested that the establishment and success of polyploidy are influenced by abiotic and biotic stress (272).

Small genomes are significantly overrepresented among invasive taxa (256), supporting the large genome constraint hypothesis (139). This hypothesis posits that species with small genomes achieve a much wider range of trait states than species with large genomes, and many traits associated with large genomes are not compatible with the characteristics of successful invaders (256). Small genome size is associated with faster growth (74, 145). However, Meyerson and colleagues (176) found that larger monoploid genome size in *P. australis* was associated with better-defended leaves, potentially suggesting a trade-off between defense and growth rate. Studies exploring the association of naturalization success with small genome size indicate that this is a potentially powerful trait for predicting non-native species' success in stressful environments in dry regions (178).

Intra- and interspecific hybridization is another mechanism that induces several types of genetic and epigenetic events that potentially lead to novel traits, new species, and increased invasiveness (104, 237, 242), which can affect the reproductive and growth potential of hybrids and

their successful establishment (112, 187). Hybridization is linked to variation in traits that typically promote invasiveness (112, 242), such as increased fecundity and size (112), although these relationships may not be causal (187). Moreover, transient hybridization with a resident species or an earlier invader may allow a species to overcome low genetic diversity resulting from founding events (242). This can play a role with regard to Allee effects and overcome constraints associated with initial low densities even without enhancing local adaptation; such a mechanism has been proposed for the replacement of an earlier invader *Cakile edentula* by later-arriving *Cakile maritima* (175).

How polyploidization and hybridization affect invasion success will depend on introduction histories (historic versus recent) and whether the polyploids and/or hybrids occur within a founding population or arise following introduction into new environments (187, 258). Positive and negative long-term implications of hybridization generally remain poorly understood, and they could result in genomic extinction by disrupting local adaptation (97).

3. ECOSYSTEM INVASIBILITY

3.1. Edaphic Conditions: Disturbance and Resource Availability

Several hypotheses have been proposed to explain invasion success in relation to the characteristics of the recipient ecosystem or the evolutionary histories and functional roles of its species (10, 38) (**Figure 1**). Invasibility can be quantified as the probability of successful establishment per introduced propagule (50). It should not be confused with the level of invasion (163), which is a measure of the extent to which a system has been invaded and varies over time as an invasion progresses (29, 34, 35, 98). Yet, most studies examining ecosystem invasion refer to the level of rather than the vulnerability to invasion, which is often confounded by propagule pressure and residence time of the invaders (5).

The concepts of species invasiveness and the invasibility of recipient communities (163) and ecosystems have long been primarily examined separately (144, 234, 261). However, the importance of plant biological properties for invasion success varies with the characteristics of the recipient ecosystems (119), which influence invasibility and resilience against invasion (61, 234, 273). Thus, some species are likely to become invasive in certain ecosystems but not in others, and their success may vary even within the same ecosystem type, although the evidence for this is scarce.

Properties of recipient ecosystems that may affect their invasibility include (a) resource availabilities and their temporal fluctuations, disturbance regimes, and environmental heterogeneity; (b) the diversity and species richness of native plant communities that are linked to the biotic resistance to invasions or their functional or evolutionary similarities to incoming non-native species; and (c) the presence (or absence) of natural enemies and mutualists.

Invasibility has been strongly linked to the disturbance regime of recipient ecosystems (29, 49) (**Figure 1**). Natural or human-induced disturbances typically promote invasibility through major changes in resource availability (49, 78, 106), displacement of native plant species, and formation of vegetation gaps that create new opportunities for rapid colonization by non-native plants (29, 106). By resetting succession and increasing resource availability, such disturbances favor the establishment and spread of non-native plants that acquire resources more effectively than co-occurring native species (known as the disturbance-mediated hypothesis) (28), rapidly respond to temporary increases in resources, and benefit disproportionately more from such increases than native species (11, 78, 81, 277). It has been argued that invasion-facilitating disturbances are those that alter historical regimes of disturbance, resulting in changes in turnover rates or fluxes of resources (e.g., space, nutrients, or light) in a system, and not disturbances per se (248), although the

Invasional meltdown:
a phenomenon
whereby non-native
species facilitate one
another's
establishment, spread,
and impacts

different components of disturbance regimes at the ecosystem level are often not distinguished in invasion studies.

Naturalization is positively related to ruderal and competitor strategies and negatively to stress tolerance (94) for all life forms but trees (99). In systems that experience frequent and severe disturbances, ruderal species tend to prevail over native competitors and stress-tolerant species in early successional stages (29, 183). Ruderal species are able to rapidly exploit windows of opportunity created by disturbances and thus avoid competition but can be good competitors too (94). The presence of native species that respond rapidly to disturbances confers some resistance to invasions (90). Yet, native ruderal species adapted to disturbances are often unable to colonize disturbed areas as successfully as non-natives (263), and the competitive ability of native communities is generally reduced by extreme disturbances (161) that favor colonization by opportunistic non-native species (245).

A positive relationship between disturbance and invasibility is most often reported in productive, nutrient-rich ecosystems (109, 183). Accumulating evidence indicates that both increases and decreases in resources are strongly associated with higher performance of invaders, while native plants vary in their responses (11). However, disturbances that decrease the availability of resources are expected to promote resistance to invasions by the recipient communities (142). In general, fluctuations in available resources (49), including pulse events (106), disrupt plant–plant interactions, especially in systems where the natives are better adapted to low-resource or stressful conditions. This is the basis of the fluctuating resource availability hypothesis (49), which does not imply any specific relationship between the diversity of native communities or functional/phylogenetic similarities in resource use between the non-native and native species (see Section 3.2). Catford and colleagues (29) pointed out that intermediate levels of disturbance, which are expected to maximize plant diversity (according to the intermediate disturbance hypothesis), may have different effects on the diversity of native and non-native species. The different responses are attributable to several interacting factors, including human-mediated dispersal, the overrepresentation of early successional species in the non-native species pool, the tendency for fast-growing species to profit most from enemy release, and increased disturbance levels in human-modified habitats (29).

Low-resource and stressful ecosystems are traditionally regarded as less invasible (35, 61, 226), but many have become invaded by non-native plants (79–81, 131, 282). Preadaptation and rapid evolutionary changes might be one cause (see Section 2.3). Again, the release from stressful conditions or natural enemies, high environmental heterogeneity (i.e., the environmental heterogeneity hypothesis) (28, 174), and disturbances that disrupt competitive interactions between non-natives and natives can partly account for the ability of invasive plants to colonize low-resource or stressful ecosystems. In low-resource ecosystems, any temporary increase in nutrient levels from natural or anthropogenic disturbances can compensate for the negative effects of resource competition with native species (58, 90) and may promote invasion, assuming that fluctuations in resources coincide with propagule availability (49).

The presence of multiple non-native species may affect invasibility and result in invasional meltdown (250), which occurs when positive interactions among invaders initiate positive population-level feedback that amplifies their impact (82, 302) or facilitates secondary invasions (89, 186, 192). This phenomenon is especially important when invasive species promote major biotic and abiotic changes in the recipient communities, such as soil legacy effects and changes in biogeochemical cycles (82, 89, 129, 186, 192). In this respect, it is important to distinguish between invaders that are only passengers of wider environmental pressures from those that are drivers of changes that can facilitate their own persistence and spread (288).

Proximity to highly modified ecosystems, such as crop fields and forest plantations, which act as major sources of non-native propagules (232, 282, 294), inevitably affects vulnerability to plant

invasions. Urban ecosystems are exposed to a high propagule pressure and repeated local introductions from building activities, transport, gardening, and other activities (211). Changes in land use and uses of non-native plants in agriculture and forestry that result in landscape fragmentation and degradation represent further disturbances at the landscape level. These phenomena have contributed to the range expansion of many non-native species (210, 282), including invasion into ecosystems traditionally regarded as less invasible, such as forest remnants (282), by creating habitat edges that can be colonized by non-native species (106, 173).

Roads, rivers, and canals that act as dispersal corridors of propagules also increase ecosystem invasibility (35, 44, 282), even in species-rich ecosystems. Flooding facilitates invasions in riparian and other ecosystems subject to recurrent floods (108) through a temporary increase in available nutrients and dispersal of propagules (41, 204, 231).

Roads and railways provide opportunities for the establishment and spread of non-native plants, even in protected and species-rich ecosystems (151, 281). This is especially true in mountain ecosystems globally, which are threatened by climate change, greater anthropogenic land use, and new propagule introductions, which provide opportunities for increased colonization along elevational gradients (44, 173, 205, 209, 281). Although the occurrence of non-native species typically decreases with elevation (173, 205, 281), a warming climate may create opportunities for non-native plants near roads to spread further upwards (44, 281). Recent evidence from mountain roads in seven regions worldwide suggests that invasive species colonizing roadsides differ in species traits from those spreading into adjacent natural vegetation (173); invasive species along roadsides were long-lived, nonruderal species with less efficient dispersal compared to those colonizing the adjacent vegetation, which were instead shade and moisture tolerant. Though this seems counterintuitive, it confirms roads as corridors facilitating the dispersal of species that do not necessarily possess traits for long-distance dispersal. Recreational trails have also been found to act as habitats and corridors for the movement of non-native plants (157); this represents a rising threat to protected areas as the importance of tourism and recreational activities increases (71, 157).

3.2. Biotic Interactions and Invasibility

Biotic interactions between non-native plants and resident plants and organisms from other taxonomic groups have a strong influence on the invasibility of recipient ecosystems (268). While most hypotheses refer to antagonistic interactions such as competition from the resident plant species or the role of herbivores, predators, and pathogens, evidence from the past two decades points to the need to include positive (facilitative or mutualistic) interactions as important mediators of community invasibility (268).

3.2.1. Importance of competition and facilitation. The failure of many invasive non-native plants to become weedy in their native ranges indicates that they interact in novel ways with the biota in recipient ecosystems in their invaded range (38, 203). The characteristics of the recipient plant communities determine the quality and strength of competitive interactions and thus the resistance (or vulnerability) to plant invasions. Hypotheses on the biotic resistance to (or acceptance of) plant invasions of recipient communities focus on (*a*) community diversity (mainly species richness) and (*b*) functional or phylogenetic similarity or dissimilarity between native and non-native plants. Many of these hypotheses relate the invasibility or resistance to differences in the competitive ability of the native and non-native species, especially through acquisitive rather than conservative traits (80, 90, 286).

The biotic resistance hypothesis posits that ecosystems supporting high native diversity are more resistant to plant invasions than species-poor ones [see Traveset & Richardson (268) for

Invasion paradox: the positive correlation between native and non-native plant species at the landscape and regional scales that defies predictions of biotic resistance

a comprehensive treatment of this topic]. One version of this idea is the diversity–invasibility hypothesis, which links species diversity to biotic resistance, typically invoking mechanisms of competition for available resources, as suggested by Davis and colleagues (49). This hypothesis has been mainly tested by assessing the relationship between native and non-native species richness. This relationship is strongly context dependent and varies with the spatial scale of the study, in observational versus experimental studies (9, 49, 85, 155, 194, 268), and with environmental conditions, such as environmental stress (280), productivity (47), and disturbance (156). In general, the sign of this relationship changes from negative to positive with increasing spatial scale (77, 247, 265), constituting the so-called invasion paradox. This paradox reflects that different processes act at different spatial scales, including biotic interactions at fine scales, and that native and non-native species respond to large-scale factors such as soils, geology, or climate in the same way (77, 140). Recently, Ernst and colleagues (64) used a 15-year, 15-site grassland data set to show that the invasion paradox dissolves when phylogenetic and temporal perspectives are invoked. More phylogenetically diverse communities had higher abundances of invasive species. However, with increasing time, the phylogenetically diverse communities became most resistant to invasion, highlighting that diversity–invasibility relationships need to be examined over time (64).

The observation that native and non-native species richness are positively correlated in some ecosystems has informed the biotic acceptance hypothesis (or the rich-get-richer hypothesis) (11, 77, 255); at large spatial scales native–non-native species-richness relationships are always positive (206) since the diversity of both groups tends to increase as landscape heterogeneity and habitat diversity increase (255).

An observed negative relationship between native plant diversity and plant community invasibility (9) has been explained by two major mechanisms: the sampling effect (264) and complementary resource use (155, 264). The sampling effect is based on the premise that, in more diverse plant communities, there is a high probability that good competitors are present, making a community less invasible. Complementarity has been attributed to the higher stability of diverse communities (i.e., the diversity–stability hypothesis) (264) since they occupy more space, generate more biomass, and/or use available resources more completely (45, 49). Empty ecological niches, which may facilitate invasions by non-native species occupying different ecological niches with respect to their use of limited resources, are thought to be less available in diverse plant communities (known as the empty niche hypothesis) (61). To unify theories on invasiveness and invasibility, MacDougall and colleagues (167) suggested that this issue should be examined with regard to niche and fitness differences. The presence of empty niches or trait space (180) unoccupied by native species, resulting from differences in resource use (156), would facilitate the establishment of non-native species through competition avoidance. By contrast, in the absence of niche differences, fitness differences (i.e., differences in the competitive ability, fecundity, or susceptibility to predators and pathogens) would result in competitive exclusion by species with the highest average fitness.

A more complex perspective on the diversity–invasibility relationship distinguishes strong invaders, which become dominant in the recipient communities, from weak invaders, which occur at low densities (194). The expectation based on this distinction is that at local scales, native species richness will vary negatively with the richness of strong invader species and positively with the richness of weak invader species, as observed for grassland communities invaded by bunchgrass *C. maculosa* in western Montana, USA (194). There is also evidence that native species abundance, rather than species richness, regulates resistance to plant invasions and that intermediate disturbances provide the greatest resistance because they promote the greatest native species abundance (32). In this respect, dominance by one or more native species may affect the diversity–invasibility relationship. Grime (95) warned about linking invasibility exclusively to plant diversity since most

of the plant biomass (a proxy for the resources used by a community) is often attributed to a small number of dominant species, even in species-rich communities. Since dominance is important in regulating community and competition dynamics (95, 253), the presence of one or more dominant native species may facilitate plant invasions through the amelioration of stressful or suboptimal conditions (253, 278) or provide resistance by exacerbating resource competition (253). Nonetheless, available evidence suggests that non-native dominants are often competitively superior to native dominants (16) or are better at suppressing the diversity of native species compared to native dominants (110).

Other processes affecting invasiveness and the diversity–invasibility relationship include the abovementioned opportunities for inter- and intraspecific hybridization and genetic admixture, the presence of multiple non-native species that may result in invasional meltdown (250), and positive interactions (facilitation) with native plant species (31, 164, 230). Facilitation can have especially important effects on invasibility in stressful environments (164). For instance, recent evidence shows that facilitation by native shrubs in arid ecosystems can both accelerate the invasion process and amplify the negative effects of non-native species on native annuals through indirect shrub-mediated interactions (164).

In contrast to the diversity–invasibility hypothesis, which focuses on how community-level metrics (i.e., diversity or richness of the recipient communities) predict invasion success, other hypotheses focus on how similarities in functional traits (85, 263) or phylogenetic relatedness between non-native and native species affects ecosystem invasibility (21, 48, 138). These hypotheses cast an eco-evolutionary perspective on plant invasions (38, 62) and are based on mixed evidence (21, 48, 138) that invasion success is more or less likely by non-native species that are either distantly (as in Darwin's naturalization hypothesis) (45) or closely related to native species (53, 199). Darwin's naturalization conundrum (53) refers to how Darwin (45) provided two seemingly opposing views regarding the relatedness of non-native and native species. Given the importance of environmental filtering in selecting traits, non-native species closely related to native ones should be more likely to become established because they share preadaptation to local conditions (i.e., the preadaptation hypothesis). However, if competition is important, we should expect that intense competition among closely related native species would favor the establishment of distantly related non-native species via a differential use of resources and the exploitation of different ecological niches, as in the competition-relatedness hypothesis (21, 199). This apparent inconsistency is largely explained by the fact that these relationships have been examined at different spatial and temporal scales and at different stages of invasion; many different mechanisms drive patterns that are observable at the different scales and invasion stages (18). For instance, vegetation data from the USA indicate that the presence of native species that are closely related to potentially invasive species is more likely to predict invasion success at larger spatial extents than at finer, local spatial scales, where competition for the same pool of limited resources tends to be stronger among closely related species (199). There, non-native species and their close native relatives were found to be more likely to co-occur at larger spatial extents than at smaller, local spatial scales (199). Moreover, in harsher climates, non-native species are more closely related to native species since adaptations to harsh environments tend to be phylogenetically conserved (103), while the effect of competition is generally stronger in more homogeneous and benign environments (199).

Functional and phylogenetic relationships between native and non-native plants can change during the invasion process. Since selection pressures vary over time, postintroduction evolutionary processes and coevolutionary processes in the native species may alter the strength and direction of competitive interactions between non-native and native species over time (18). Moreover, the significance of competition in shaping the recipient communities depends strongly on the timing of any competitive interaction (90, 293). A high (or superior) capacity to compete

Facilitation:

ecological interactions between two organisms that benefit at least one of the participants and cause harm to neither

for resources may be less important or irrelevant if native and non-native species are displaced phenologically, such that non-native species germinate or initiate vegetative growth earlier than co-occurring native species, thereby reducing the intensity of competition with native species (79, 90, 293) or completing their life cycles earlier (136).

In a comprehensive review of the functional similarity approach in invasion community ecology, Gallien & Carboni (85) showed that at fine spatial scales, the resistance of plant communities to invasion tends to increase with the diversity of native species and similarities between the native and invasive species. Interestingly, they found conflicting evidence for differences in community assembly processes in the native versus non-native ranges of an invader, suggesting that the processes of filtering differ at home and abroad. This study confirmed that the role of trait differences is strongly context dependent, varying across plant communities, along environmental gradients (124), with the stage of the invasion process (80, 85), and with life form (80).

Evidence that communities with high phylogenetic diversity are more resistant to plant invasions is limited (48, 138). Phylogenetic relatedness with the native species in the recipient communities is not a consistent predictor of invasion success at fine spatial scales (19), and local environmental conditions, community types, and propagule pressure interact in determining invasion success (75, 138). In this respect, the ecological imbalance hypothesis stipulates that non-native species originating from regions with highly diverse evolutionary lineages could be more likely to become invasive in less diverse regions (76) through an expected higher competitive ability (75), placing emphasis on the evolutionary characteristics of both the recipient region and potential donor regions (73). This hypothesis was recently supported by findings that, in natural areas in New Zealand, phylogenetic diversity of the native range was one of the best predictors of invasiveness in forests, while it declined in importance in more disturbed habitats (75). In this study, Fridley and colleagues (75) found support for the ecological imbalance hypothesis and Darwin's naturalization hypothesis, although, in the latter, the role of resource competition as a predictor of invasiveness was not important.

3.2.2. The role of natural enemies. The presence (or absence) of natural enemies and mutualists affects invasion success and invasibility, especially at the initial stages of invasion. Popular explanations attribute invasion success to the release (the enemy release hypothesis) (24, 45, 61, 135) or partial release (the enemy reduction hypothesis) (39) from natural enemies (e.g., specialist herbivores, pathogens, and parasites) in the recipient communities. A decrease in regulation by herbivores and other enemies has been linked to dominance and widespread distribution (39), although Colautti and colleagues (39) argued against an uncritical acceptance of this hypothesis since it depends on the extent to which natural enemies regulate demographic processes. It is also possible that introduced enemies of non-native plants might be less harmful in the invaded than in the native range due to better conditions the invaders encounter in the former (the enemy inversion hypothesis) (39) or might be more harmful to co-occurring native than to co-occurring introduced species (the enemy of my enemy hypothesis) (63).

Release from specialist enemies could promote evolutionary shifts toward allocating fewer resources to defense and more resources to enhanced competitive ability through genetic changes [the evolution of increased competitive ability (EICA) hypothesis] (14, 24). Support for the full EICA hypothesis is mixed (15, 67, 170, 239). A meta-analysis found broad support for genetically based changes in plant defense and competitive traits after introduction into new ranges, but not in the manner proposed by the EICA hypothesis, suggesting that evolution occurs as a result of plant introduction and population expansion in invasive plant species, although it might not necessarily result in increased size and competitive ability in the introduced ranges (37). It has also been observed that the effects of both intraspecific and interspecific competition should be accounted

for when testing the EICA hypothesis (15) since invasive populations may have lower fitness (276) and reduced competitive ability under intense intraspecific competition. Indeed, one prediction is that non-native populations may evolve reduced intraspecific competitive abilities (i.e., the evolutionary reduced competitive ability hypothesis), allowing the conservation of resources needed to compete against native species in the introduced range or to use for other defensive processes such as the release of allelochemicals (213) or improvement of tolerance to herbivory (15). Evidence for the evolution of increased intraspecific competitive ability in the invasive clonal herb *Alternanthera philoxeroides* suggests that interactions among the same genotypes may shift from competition toward facilitation following introduction (305).

It has been argued that the release from enemies hypothesis is too simplistic to provide a helpful explanation for invasion success (39, 244). Non-native plants may escape some enemies but not others, and the identity of the enemies, and whether they are generalists or specialists, is very important in determining invasion success (130, 165, 202). Invasive non-native plants are expected to be released from specialist herbivores but to encounter biotic resistance from resident generalist herbivores, with evidence that non-native plants evolve decreased defense against the former and increased defense against the latter (304) (i.e., the shifting defense hypothesis) (130). While non-native plants are susceptible to native generalist herbivores (biotic resistance), non-native herbivores may facilitate both the abundance and species richness of non-native plants (201). Native consumers may even prefer non-native over native species, thereby increasing resistance against invasions (125, 201, 202). If non-native species have not coevolved with consumers found in the introduced range (termed new associations) (36), they will lack effective defenses against them (as in the increased susceptibility hypothesis) (39), although this increased susceptibility to enemies associated with postintroduction evolution at the expense of defensive abilities does not preclude non-native populations from outperforming native ones, as shown for the invasive herb *Silene latifolia* (291). Release from natural enemies is a dynamic process, and as the range size and residence time of introduced species increase, they ultimately fail to escape enemies (244). The native biota can also evolve in response to the presence of invasive plants, and some invasive plants retain or recover their natural defenses over time (241). Highly invasive species have even shown a greater prevalence of natural enemies than phylogenetically related noninvasive introduced species (200).

3.2.3. Mutualism. The diversity of mutualists such as pollinators, seed dispersers, and microbiota forming symbioses with plant roots may strongly influence ecosystem invasibility (152, 169, 214, 230, 292). By contrast, the absence of coevolved mutualists in the introduced range might have a negative effect on non-native species, thereby conferring resistance against certain invaders (known as missed mutualists) (179). The net effects of soil microbial communities in the introduced range determine failure or success, depending on the relative strength of pathogenic (negative) effects (as in the enemy release hypothesis) as opposed to mutualistic (positive) interactions (as in the enhanced mutualist hypothesis) (224) with soil microorganisms in the introduced range (297). Not only do invasive plants interact with the native soil biota, but they may also promote changes in the soil biota (292). Plant invasions often increase the diversity of bacteria (but not fungi), with possible effects on nutrient cycles, enzymatic activity, mineralization rates, and soil carbon and nitrogen content (266). Introduced mutualists, such as seed-dispersing ants, have been found to promote the dominance of non-native plants (214), supporting the invasional meltdown hypothesis. Moreover, invasive populations have been shown to suppress soil mutualists in introduced ranges more aggressively than mutualists in their native ranges, resulting in a competitive advantage over mutualist-dependent native species (as in the mutualism disruption hypothesis) (22), via either negative feedback (279) or novel chemical weapons (23, 102).

Indirect interactions mediated by organisms such as herbivores, pollinators, seed dispersers, or the soil biota can mitigate or exacerbate direct plant–plant effects and affect invasibility and invasion success. Examples of indirect interactions include competition for shared pollinators (287), which often results in reduced visitation of pollinators to native species in the presence of a non-native species; such effects may be exacerbated by the dominance of invasive species in a community [see Traveset & Richardson (268) for a comprehensive review of this topic]. Apparent competition between plants occurs when one species alters the abundance or distribution of consumers and thus the consumption of the other plant species; this type of interaction between native and non-native plants has been most frequently examined in plant–herbivore systems (287), and there is evidence of negative effects for native species (90, 287). However, non-native species could have positive effects on the competitive ability of native species by reducing the pressure from generalist herbivores, although empirical evidence of this is lacking.

3.3. Ecosystem Invasibility and Propagule Pressure

To assess the invasibility of an ecosystem, the number and frequency of propagules introduced (propagule pressure) and the fraction of propagules that survive must be jointly considered (163, 233). Based on a meta-analysis of the relationship between propagule pressure and the successful establishment of non-native herbaceous species and long-lived trees, Cassey and colleagues (26) concluded that propagule pressure is the most consistent and strongest determinant of non-native species establishment. Propagule pressure can influence invasion success in many ways: multiple introductions, environmental preadaptation and human commensalism, high gene flow along invasion routes, and human-induced dispersal (69, 154). High propagule pressure has been shown to increase the probability that a non-native species will find opportunities to become established, such as a suitable microclimate, an empty ecological niche, or a microhabitat free from enemies (50, 226, 289), and can accelerate range expansion (227). An increase in propagule pressure is expected to favor colonization in low-stress environments, where nutrient availability is high and biotic resistance weak, as shown for the annual ruderal *Arabidopsis thaliana* (111).

3.4. Ecosystem Invasibility Under Global Changes

There are major concerns about how human-induced climatic changes, increasing atmospheric CO₂, and nitrogen deposition will affect ecosystem invasibility, the trajectories of plant invasions, and the resilience of the recipient communities. Long-term implications of the influence of global changes on plant invasions are speculative, given the many unknowns. Both non-native and native species might shift, shrink, or expand their ranges and colonize new areas and ecosystems in response to climate changes (115, 212). This can lead to the creation of new assemblages of co-occurring taxa, affecting the biotic resistance of the new communities and disrupting biotic interactions, which could be advantageous to either the non-native or native species (283). There is evidence that these human impacts alter disturbance and resource dynamics (58, 101, 115, 270) and disrupt biotic interactions with enemies and mutualists (115, 268), although the long-term direction of these changes remains unclear. Climatic changes may also alter the phenology of native species, thereby opening phenological opportunities for non-native species establishment under low competition (90, 113, 293).

Evidence from mountain ecosystems, which are particularly vulnerable to the combined effects of a warming climate and increasing human activity, indicates that non-native plants have expanded and will continue to expand their range at higher elevations under the warming climate (44, 209, 281). In the European Alps, non-native plants are spreading upwards approximately twice as fast as natives, with species in both categories spreading upwards faster than would correspond to the

current velocity of climate change because the spread is accelerated by the proximity to roads and long-distance dispersal events (44). For non-native clonal plants, evidence from protected areas suggests that under a changing climate, the risk of invasions, compared to that of nonclonal species, increases in biomes located at high elevations and high latitudes and decreases in lower elevations and in tropical and subtropical biomes, where asexual reproduction may be a less successful trait (284).

Because rapid postintroduction evolutionary changes and/or broad environmental tolerance characterizes many invasive plants, they may respond rapidly to climatic changes (66, 87, 286). Yet, evidence for climatic adaptation in resilience traits is mixed (66). Available evidence based on demographic processes suggests that plant species that are less likely to be impacted by climate warming will be those whose seeds can survive in persistent soil seed banks that are not rapidly depleted by temperature increases or other related environmental changes (91). Since the capacity to accumulate persistent seed banks is an important trait associated with naturalization and invasiveness (88), it is possible that many invasive species may be more resistant and resilient against climatic changes through dispersal in time, although the buffering effects of seed banks may be only temporary (91). Although information on the potential effects of climate change on plants is available only for a small proportion of species and suffers from a geographical bias, it is becoming increasingly evident that invasive species respond to climate change through decreased seed dormancy, earlier germination, and increased germination percentages (115).

4. MOVING FORWARD IN INVASION ECOLOGY RESEARCH

Much progress has been made in identifying functional traits that predispose species invasiveness and the ecosystem properties that increase vulnerability to invasions. However, attempts to find a common recipe for invasion success for the global flora are unlikely to succeed. Indeed, seeking a one-size-fits-all answer is counterproductive. Species in different taxonomic groups achieve success in invasiveness in very different ways (189, 233, 236), and the contribution of species traits to invasiveness varies across life forms (80, 84, 219, 222) and ecosystem properties. Moreover, there is a taxonomic introduction bias because not all species or higher taxonomic groups have been moved around the globe to the same extent, resulting in different opportunities to become naturalized and/or invasive (133, 172, 193, 222, 236). This pattern has also biased the current understanding of traits associated with invasiveness.

The field of invasion ecology suffers from too many theories and too little empirical data for many of them (127). There is an absence of comparative tests of different theories, and some studies have tested some theories only partially; this is the case of the enemy release hypothesis, which is typically examined by focusing on one or a few enemies rather than exploring the roles of all enemies, both specialists and generalists, that an invasive species acquires in the introduced range. Therefore, some hypotheses are supported by little empirical evidence and the support is even declining over time (127).

From this admission, it follows that we need more data, but not just any data. We need large-scale experiments, combining biogeographical and ecological approaches, that are built on global collaboration and designed to elucidate the role of drivers of invasiveness and their interactions in defined environmental and different socioeconomic contexts (e.g., 68). International networks for invasion science have been recommended to address questions that require a biogeographic approach, such as evaluating the role of biogeography on the susceptibility, resistance, and resilience of ecosystems against invasion (267); predicting the probability of an invasion and the vulnerability of ecosystems to plant invasions under global change (2); and the role of adaptation and evolution in determining invasion success (196).

Invasion syndrome:

a combination of pathways, non-native species traits, and characteristics of the recipient ecosystem that results in predictable dynamics and impacts

Another challenge is to incorporate traits that are missing from our models because this knowledge is restricted to a limited number of species, and screening for complete floras is not available. For example, in the last decade substantial progress has been made in predicting invasiveness by including knowledge of the persistence of seeds in natural seed banks (88) and genome size (256), which both play pivotal roles in many plant invasions but have long been ignored because of the lack of information. Evidence at a global scale shows that the capacity to produce persistent seeds better captures the ability of a species to spread through time and space than traits such as seed mass and seed dormancy (88). The roles of many other traits in the various stages of the invasion process (and not only correlations between mean trait values with the naturalization or invasion status of a species) remain to be discovered, explored, and integrated into models. Among the priorities are traits involved in plant–microbe interactions, not only in the rhizosphere but also in the phyllosphere, as well as endophytes found within the plants themselves.

Molecular tools have made important contributions to our understanding of aspects of plant invasiveness in the last two decades, but many exciting opportunities remain, for example, to determine the potential role of horizontal gene transfer in rapid evolution during invasions. The fields of metabolomics and transcriptomics will enable greater functional insights into the evolutionary shifts following the naturalization of species in new regions and under different selection pressures.

More options for yielding novel insights into plant invasiveness lie at the interface between spatial scales. For example, new technologies for remote sensing provide novel avenues for viewing and studying invasions at multiple scales of space and time. A rocking approach that continuously shifts focus between stages and scales (229) has the potential to provide new perspectives on, for example, the role of long-distance dispersal in initiating and sustaining plant invasions.

Much uncertainty pertains to the temporal dimension of plant invasions, and evidence is accumulating of long-established invasive populations being replaced by native or other non-native species or of decreasing impact of the invader on species richness over time (56). While a suite of species traits (e.g., those related to the ability to acquire or conserve resources and maintain high plasticity) indeed characterizes invasion success in many ecosystem types, it remains unclear whether the benefits of these traits will persist over time or are only transient, especially under global environmental changes or after major disturbance events. Some opportunistic traits that provide initial advantages over natives may, in fact, pose a risk for survival in a community, such as those leading to early germination or growth in the growing season. Long-term studies evaluating demographic and evolutionary processes under varying environmental conditions are needed to evaluate how invasive species may facilitate their own growth or that of other alien species through altering the biotic and abiotic conditions of the introduced ranges.

A way to side-step the limitations of separate studies of species invasiveness and community invasibility is to adopt the invasion syndromes approach (144), which aims to identify combinations of “pathways, [non-native] species traits, and characteristics of the recipient ecosystem which collectively result in predictable dynamics and impacts, and that can be managed effectively using specific policy and management actions” (189, p. 1806). This approach recognizes that some cross-taxon and cross-habitat generalizations are legitimate, robust, and useful (208), albeit only within a certain shared context (143). Compared to other syndrome approaches, such as the domestication syndrome (1) or the pollination syndrome (51), this approach goes beyond identifying shared characteristics of a certain taxon or taxonomic group; it encompasses features of invaded ecosystems and the causes and pathways that lead to the introduction of non-native taxa. Examples of this approach include syndromes identified for invasions of cacti through clonal fragmentation in arid ecosystems, plant invasions in the mountains, and invasions by tall-statured grasses (189) (**Figure 2**).

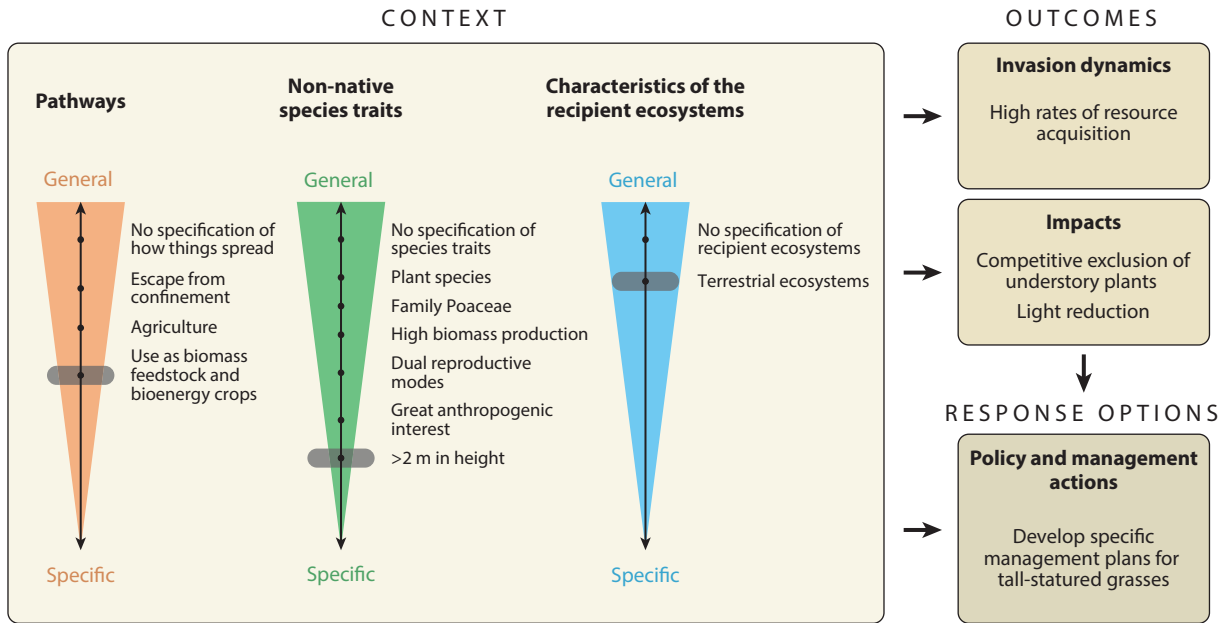


Figure 2

Example of an invasion syndrome: the tall-statured grasses syndrome. An invasion syndrome is defined as a combination of pathways, alien species traits, and characteristics of the recipient ecosystem that collectively result in predictable dynamics and impacts and that can be managed effectively using specific policy and management actions. The invasion context is displayed on three vertical axes (*triangles*) ranging from (*top*) general to (*bottom*) specific. Grey sliders indicate the level of generality/specificity of each axis (pathways are in *orange*, species traits are in *green*, ecosystem properties are in *blue*) within a syndrome, while dots indicate the property within each axis that is known to influence the syndrome. The positions along the axes (*grey sliders*) are adjusted so that all invasion events within the selected context result in similar outcomes and response options. For it to be meaningful, the shared characteristics (pathways, alien species traits, and characteristics of the recipient ecosystem) within a syndrome must result in predictable outcomes (regarding invasion dynamics and impacts) that can be best managed using similar management or policy responses. In this example, non-native species traits vary from general to specific, while the characteristics of the recipient ecosystems are broadly defined. Tall-statured grasses reach heights of at least 2 m and share similar pathways of introduction in the non-native ranges (introduction as biomass feedstock and bioenergy crops). Their invasion success is attributed to traits such as high biomass production and accumulation, dual reproductive modes, and a generally economic interest. They can invade different ecosystems (grasslands, wetlands, and forests) and their impacts on native communities include competitive exclusion of understory plants and light reduction through high rates of resource acquisition. Figure adapted from Novoa et al. (189) (CC BY 4.0).

Since ecological opportunities and barriers can be formed dynamically and adaptively in response to the ecological novelty created by biological invasions, Hui and colleagues (120) recommend that the barrier scheme of the invasion continuum (13, 180) be expanded to account for the dynamic complexity of ecological networks (119), including species-specific eco-evolutionary dynamics (118). If we consider persistent invasions in the context of trait-mediated biotic interactions as ensembles of evolutionary games in an open-adaptive system, the invasiveness of an introduced species can be precisely and unambiguously defined and quantified as the per capita population growth rate when rare (190); invasibility maps the terrain of positive invasiveness in the trait space. This approach opens avenues for exploring links between invasiveness and diverse ecosystem structures (124).

Another promising approach to model invasion success and account for context dependency is the Macroecological Framework for Invasive Aliens (MAFIA) (215). This framework merges insights on invasions by using three interacting classes of factors—non-native species traits, location

Ecological networks:

a web of coevolving and cofitting interactions among species in an ecosystem

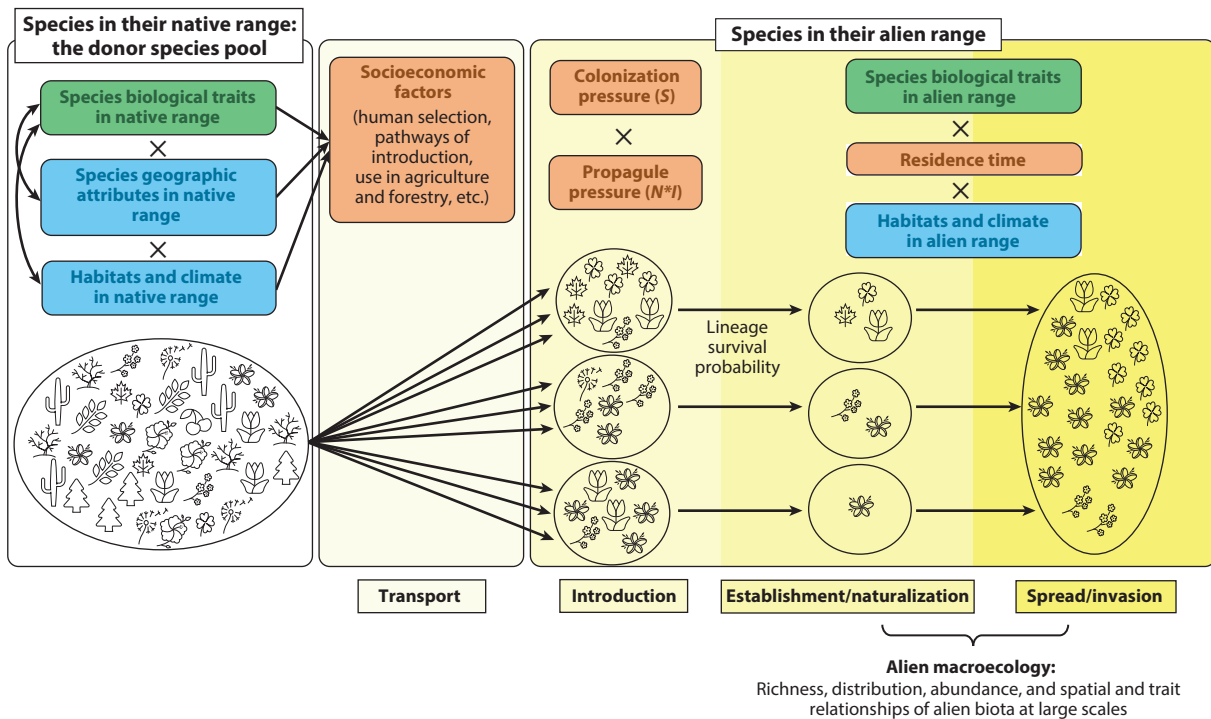


Figure 3

The Macroecological Framework for Invasive Aliens [Pyšek and colleagues (215)]. Traits of non-native species (termed alien in the scheme), including their values in the native range, are shown in green, location characteristics are in blue, and event-related factors are in orange. Individual factors are shown as operating along the introduction–naturalization–invasion continuum. Species geographic attributes and habitat and climate in the native range affect both alien species traits and event-related socioeconomic factors by influencing the probability that a species will be transported by humans from its native range. However, they are not directly related to the location characteristics in the introduced range. Lineage survival probability is the probability that any of the introduced non-native individuals leaves a surviving lineage, that is, founds a population. Abbreviations: I, number of introduction events; N, number of individuals introduced per introduction event; S, number of species introduced. Figure adapted from Pyšek et al. (215) (CC BY 4.0).

characteristics, and factors related to introduction events—to explicitly map these interactions onto the invasion sequence from introduction to naturalization to invasion (215) (**Figure 3**). MAFIA accounts for socioeconomic factors and propagule/colonization pressure, which ultimately play a key role in driving invasion success (12, 251), and introduces the biogeographical dimension of invasiveness by accounting for species traits, ecology, and performance in the native range and how these characteristics change after introduction to a new region. An example of the application of this framework is a study of European plants that have become naturalized in North America (220) where, besides time since introduction and propagule pressure in both ranges, the naturalization success most strongly depended on the breadth of habitat niche that a species occupies in its native range. Species traits, specifically a persistent seed bank and long flowering period, had only an indirect effect on naturalization success, which manifested via their effects on the variety of habitats occupied in the native range (220). This suggests that future research should explicitly link biological traits to the different stages of invasion and that a failure to consider characteristics of the native range may lead to overestimating the role of biological traits and result in spurious predictions of the major determinants of plant invasiveness (215).

5. CONCLUDING REMARKS

Much progress has been made over the last 20 years in identifying ecological and evolutionary drivers of plant invasions. The capacity of non-native species to proceed along the invasion continuum is mediated by complex interactions among multiple facilitating and limiting processes (28, 29) and by even more complex system feedback loops. Unsurprisingly, no single theory explains the success of naturalized and invasive plants in all contexts (62, 189, 285). Species traits (i.e., inherent factors), features of the abiotic and biotic environment, introduction histories, and associations with humans affect invasion success in diverse ways (215). The resulting context dependences (30) make it unrealistic to achieve comprehensive, mechanistic explanations for all plant invasions. Much better results emerge when invasion success is examined by focusing on target taxonomic groups (e.g., genera such as *Acacia* and *Pinus* or families such as Cactaceae), functional groups (e.g., trees or grasses), or habitats (e.g., riparian ecosystems, arid or semiarid grasslands, or temperate or tropical forests). In this respect, the invasion syndromes approach (144, 189, 208) provides a tractable roadmap for achieving reasonable levels of generalization based on incorporating the interacting factors in frameworks aimed at understanding and managing plant invasions.

Increasing pressure from human activities acting across scales, from local to global, has contributed to successful invasions even in ecosystems long regarded as resistant to invasions. Our understanding of the invasion process needs to consider that almost any ecosystem is invadable should the right propagules be introduced in a sufficient quantity and over a long enough period. Ultimately, the future distribution of both native and non-native plants will depend on how their populations respond to local- and global-level environmental changes and associated biotic changes throughout their life cycles.

Overall, the field of invasion ecology suffers from too many theories and too little empirical data to support many of them (127, 128). The use of ecological frameworks going beyond the traditional search for traits associated with successful naturalization and invasion or properties characterizing invadable ecosystems is a promising approach. Further progress can only be made by integrating species invasiveness, community invasibility, and environmental context into a new school of thought about invasions.

FUTURE ISSUES

1. No single theory currently explains the naturalization and invasion of non-native plants in all contexts, and seeking such a theory is an unrealistic aim. However, more work is needed to test multiple, rather than single, hypotheses through experiments.
2. The role of many traits at the individual and population levels in the various stages of the invasion process remains to be discovered, elucidated, and integrated into models. Traits involved in plant–microbe interactions, particularly in the rhizosphere and the phyllosphere, as well as endophytes, are a priority in this regard.
3. Large-scale experiments combining biogeographical and ecological approaches, built on global collaboration, are needed to uncover the role of eco-evolutionary processes in determining invasiveness and their interactions in different environmental and socioeconomic contexts.
4. Plant invasions must be examined at multiple scales of space and time to gain new perspectives on the importance of species traits and on long-term community dynamics in invaded ecosystems.

5. Molecular tools will continue to improve our understanding of diverse aspects of plant invasiveness as many exciting opportunities remain, such as determining the potential role of horizontal gene transfer in rapid evolution during invasions. Metabolomics and transcriptomics are promising tools to gain functional insights into the evolutionary shifts following the naturalization of species in new regions under different selection pressures.
6. Although the invasion continuum paradigm has served invasion ecology well as a foundational construct for exploring many facets of plant invasiveness, viewing invasions through the lens of network ecology has huge potential for uncovering new dimensions in the interplay between species invasiveness and community invasibility.
7. We suggest that the invasion syndromes approach is the most profitable way to proceed to achieve reasonable levels of generalization based on incorporating multiple interacting factors in frameworks aimed at understanding and managing plant invasions.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

M.G. and P.P. acknowledge fundings by the Czech Science Foundation (grant 19-20405S and EXPRO grant 19-28807X) and the Czech Academy of Sciences (long-term research development project RVO 67985939). D.M.R. acknowledges support from the DSI-NRF Centre of Excellence for Invasion Biology, Mobility 2020 (project CZ.02.2.69/0.0/0.0/18_053/0017850, Ministry of Education, Youth and Sports of the Czech Republic) and Czech Academy of Sciences (long-term research development project RVO 67985939). We thank Zuzana Sixtová for technical assistance.

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