The Ecology and Evolution of Alien Plants

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Abstract

We review the state-of-the-art of alien plant research with emphasis on conceptual advances, and knowledge gains on general patterns and drivers, biotic interactions and evolution. Major advances include the identification of different invasion stages and invasiveness dimensions (geographic range, habitat specificity, local abundance), and the need for appropriate comparators while accounting for propagule pressure and ~~introduction history~~year of introduction. Developments in phylogenetic and functional-trait research~~, and hybrid modelling~~ bear great promise for better understanding of the underlying mechanisms. Global patterns are emerging with propagule pressure, disturbance, increased resource availability and climate matching as major invasion drivers, but species characteristics also play a role. Biotic interactions with resident communities shape invasion outcomes, with major roles for species diversity, enemies, novel weapons and mutualists. There is mounting evidence for rapid evolution of invasive aliens and evolutionary responses of natives, but a mechanistic understanding will require better integration of molecular and phenotypic approaches. We hope the open questions identified will stimulate further research on the ecology and evolution of alien plants.

1. **INTRODUCTION**

The study of alien organisms, and their biotic interactions and varying invasion success is a major research area in ecology and evolutionary biology. Its motivation has always been two-fold: On the one hand, scientists and conservation managers have been concerned about negative impacts of alien organisms on native biodiversity and economy. On the other hand, since alien organisms often experience novel ecological contexts, and there is large variation in invasion success, which is at least partly explained by ecological and evolutionary processes, the study of alien species greatly advances our fundamental ecological and evolutionary understanding (Sax et al. 2007). The initial research agenda for invasion biology was set by two seminal books on the ecology (Elton 1958) and genetics (Baker & Stebbins 1965) of invasive species. Research has grown exponentially particularly in the second half of the previous century (Gurevitch et al. 2011), and invasion biology is now a mature discipline.

Within invasion biology, the study of alien plants has been particularly strong, with its findings summarized in numerous reviews (e.g., Rejmánek 1996, Pyšek & Richardson 2007). Nevertheless, our understanding of alien plant invasions, and invasion biology more broadly, has long been hampered by unclear and inconsistent use of definitions (Pyšek et al. 2004), failure to account for year of introduction and propagule pressure (~~and a lack of appropriate null models (~~Colautti et al. 2006), and use of ~~comparator groups~~comparisons of invasive species (or populations) to reference species (or populations) that do not address the research question (van Kleunen et al. 2010a). Moreover, there has sometimes been a lack of understanding of how different hypotheses in plant invasion biology are related (Catford et al. 2009). In recent years, there has been much progress in this regard.

In this review, we describe some of the major conceptual and methodological advances, and empirical studies that have improved our understanding of plant invasions. We do not provide a systematic, exhaustive review, but ~~a series of~~rather an overview of selected key topics where progress has been made, from macro-ecology and biotic interactions to evolution and genetics. Our review is accompanied by a visual summary in **Figure 1** where we indicate, for each topic, how well it has been studied so far, how consistent the results ~~were and how many open questions there still are in it~~have been from study to study, and how many questions remain open. Although this figure is clearly somewhat subjective, we hope that together with the 'way-forward' sections below, it will stimulate and guide future research on the ecology and evolution of alien plants.

2. CONCEPTUAL AND METHODOLOGICAL ADVANCES

With the rapid increase in research on alien plants, our understanding of the processes that drive plant invasions has increased considerably. Several conceptual and methodological advances have contributed to this.

2.1. The Invasion-stages Framework

Invasion biology has developed a large vocabulary with multiple terms for the same things (e.g., alien, exotic, non-native, non-indigenous), and multiple definitions for the same terms (e.g., invasive; see below). To increase clarity and consistent use of terminology, Richardson et al. (2000) proposed an invasion-stages framework with a sequence of barriers that a plant species has to overcome to become invasive **(Figure 2)**. In this framework, aliens are plant species that have passed a biogeographic barrier (e.g., an ocean) with help of humans. The aliens that have passed the subsequent environmental barrier and sometimes occur in the wild but do not form persistent populations are considered casuals. The ones that have passed the environmental and reproductive barriers, and have established wild populations that persist

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over multiple life cycles, are considered naturalized. The subset of naturalized species that have overcome the dispersal barrier and produce reproductive offspring, often in very large numbers, at considerable distance from parent plants (>100 m within <50 years; Richardson et al. 2000) ~~within the non-native range and subsequent environmental barriers they encountered~~ are considered invasive.

While the Richardson et al. framework is widely applied (3042 citations in Google Scholar, accessed 11 January 2018), definitions of ‘invasive’ vary. The Richardson et al. (2000) definition is neutral with respect to ecological and economic impacts, whereas the Convention on Biological Diversity (CBD 2000) defines invasive species as those whose introduction and/or spread threatens biological diversity. Problematic is that the latter is frequently unknown. Other definitions of ‘invasive’ are used less frequently, although they consider interesting aspects. For example, ~~(~~Alpert et al. (2000) proposed decoupling ‘invasive’ from being alien, and Hufbauer & Torchin (2007) proposed defining a species invasive when its demographic performance is higher in the invaded than in the native range. While many alien species might qualify as invasive under all these definitions, there are exceptions. Parker et al. (2013) showed that plants among ‘*100 of the world’s worst invasive alien species*’, which follows the CBD (2000) definition, perform on average better in their non-native than in their native ranges, thus meeting the Hufbauer & Torchin (2007) ‘invasive’ definition. However, there was high variability among these species in this regard. Although none of the ‘invasive’ definitions is necessarily better than the others, the use of multiple definitions has resulted in confusion, and might explain some of the apparently conflicting findings among studies. Therefore, we call for researchers to always state clearly which definition of ‘invasive’ is used. Here, we use the Richardson et al. (2000) definitions of alien, naturalized and invasive, unless stated otherwise.

2.2. The Multiple Dimensions of Invasiveness

~~The multiple 'invasive' definitions demonstrate that i~~Invasive species, as described in the literature, are not a homogeneous group. While the Richardson et al. (2000) definition of invasive primarily focu~~s~~ses on spread of the naturalized species, it also implicitly~~ also~~ assumes that the species are locally abundant (i.e., produce reproductive offspring in large numbers). Species show continuous variation in spread (i.e., range size) and abundance, ~~and~~which means that invasiveness is not binary, but is instead ~~therefore a~~ continuous ~~variable~~and multidimensional. ~~rather than a binary (yes/no) variable. Moreover, w~~~~W~~While some naturalized alien species are wide~~-~~spread, they have a low local~~ly~~ ~~abundant~~abundance~~,~~ ~~they might have a small non-native range or be restricted to few habitats~~, whereas others might have a ~~large~~ small range and ~~occur in many habitats but have sparse populations~~have a high local abundance~~. In other words, invasiveness has multiple dimensions~~ (**Figure 2**). For the related concept of ~~The idea that rarity and~~ commonness (or rarity), Rabinowitz (1981) proposed,~~ have three dimensions —~~ in addition to geographical range~~,~~ and ~~habitat specificity,~~ local population size (i.e., abundance), to also consider the range of habitats in which a species occurs (i.e., habitat generality). This idea of multiple dimensions of a species' distribution or commonness ~~— was originally developed by Rabinowitz (1981), but~~ has only recently been applied to invasiveness of alien plants (Dawson et al. 2013, Catford et al. 2016).

The different invasiveness dimensions are likely to be associated with different main barriers (**Figure 2**). Range size (spread) may be mainly determined by one or more dispersal barriers, local abundance by one or more competition barriers, and habitat generality by one or more environmental barriers. Depending on the specific research question, one could also consider~~Potential~~ ~~additional~~ further dimensions, such as ~~of invasiveness are~~ the rate of spread~~ rate~~ (Catford et al. 2016), and different categories of ecological and economic impacts,

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which would then also include the CBD (2000) definition of invasive. We believe that consideration of these different invasiveness dimensions in research on alien plants may ~~provide more consistent results among studies~~prevent researchers from mistakenly concluding that results are in conflict.

2.3. Comparative Approaches for Assessing Determinants of Invasion Success

The variety in approaches used to study alien plants and their invasion success is enormous. While there are many descriptive studies on individual invasive species, the question of what determines invasion success requires a comparative approach. Such studies are most powerful when they include many species, populations and sites (van Kleunen et al. 2014). The comparator choice is pivotal to whether the question of interest can be answered (van Kleunen et al. 2010a). Although most studies on traits associated with invasiveness have compared invasive alien to native species (Pyšek & Richardson 2007, van Kleunen et al. 2010b, Davidson et al. 2011), this cannot reveal why alien species differ in invasiveness. This requires a comparison between alien species that differ in their degree of invasiveness~~between invasive and non-invasive alien species~~, either along a single dimension or along multiple dimensions of the invasiveness continuum (**Figure 2**). When these comparisons include non-invasive alien species, ~~, though~~ it is ~~also~~ important to realize that the latter may be at different invasion stages~~. Some non-invasive aliens~~; some ~~might not~~ are not found outside of cultivation, some are just casuals and others are naturalized but not invasive~~have been introduced, and others might be introduced but not naturalized~~ (~~**van Kleunen et al. 2015b**~~**Figure 2**). As different traits might be associated with each of these stages (Dietz & Edwards 2006, Dawson et al. 2009, van Kleunen et al. 2015b), the results of the comparison between invasive and non-invasive aliens may strongly depend on the invasion stage of the latter.

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2.4. ~~Introduction History as a Null Model~~Accounting for propagule pressure and year of introduction

It seems almost trivial that alien species introduced in greater numbers or more frequently are more likely to naturalise and become invasive, and thus should be accounted for. Nevertheless, the need to account for this so-called propagule pressure has been ~~formalized as a 'null model' for invasion success~~recognized only recently (Colautti et al. 2006). Similarly, alien species that were introduced earlier should have had more opportunities to naturalize and become invasive (Rejmánek 2000). We will discuss the importance of propagule pressure and year of introduction in more detail below. However, accounting for ~~the introduction history~~propagule pressure and year of introduction of ~~an~~ alien species has been important for disentangling the ecological and evolutionary processes that contribute to plant invasions.

2.5. Darwin's Naturalization Conundrum, Scale Dependency and Coexistence Theory

There has been long-standing interest in how differences between alien and native plants determine invasion success. ~~(~~Darwin (1859) hypothesised that alien plants distantly related from the native communities are more likely to naturalize. A mechanism underlying Darwin's naturalization hypothesis (Rejmánek 1996) could be stronger niche differentiation between resident natives and more distantly related aliens (Thuiller et al. 2010). In addition, the more distantly related the alien plant is, the less likely it is that herbivores and pathogens will spill over from native residents (see Enemy Release section below). Darwin (1859) also hypothesised that alien species from genera that occur in native regional floras may be more likely to naturalize because they sha~~rre th~~e the same pre-adaptations as the related natives. These seemingly contradictory hypotheses are now referred to as 'Darwin's naturalization conundrum' (Thuiller et al. 2010).

The realization that different ecological processes act at different spatial scales ~~is helping~~might help to resolve this conundrum ~~and~~ as well as the apparent discrepancies between studies that found positive, negative or no significant relationships between naturalization success of alien plants and their ~~the mixed findings~~phylogenetic relatedness to native plants ~~-~~(Thuiller et al. 2010). Whereas abiotic environmental filtering, which requires pre-adaptation, acts at all spatial scales, biotic filtering acts only at the small scales where species interact (Thuiller et al. 2010, Gallien & Carboni 2016). Therefore, Darwin's naturalization hypothesis (i.e., the hypothesis that alien species distantly related to native species are more likely to naturalize) should only operate at small spatial scales. As the different processes might act simultaneously, the relationship between invasion success and phylogenetic distance might actually be non-linear and depend on the phylogenetic scale (Thuiller et al. 2010, Gallien & Carboni 2016). These ideas, however, still need to be tested explicitly.

Another potential reason for the mixed findings is that the expected relationship between phylogenetic distance and invasion success rests on the assumption that phylogenetic distance reflects niche differentiation due to trait differences. However, not all traits are phylogenetically conserved. Moreover, once a species has passed the abiotic environmental filter, the outcome of competition is not only determined by niche differences but also by fitness differences (Chesson 2000, Mayfield & Levine 2010). The latter also depend on trait differences (Mayfield & Levine 2010). This modern coexistence theory has only recently been extended to biological invasions and linked to Darwin's ~~Naturalization~~ naturalization ~~Conundrum~~ conundrum (MacDougall et al. 2009, Thuiller et al. 2010). While empirical studies are still rare, the recent advances in theory, tools and data for phylogenetic and functional trait analysis bear great promise to better understand invasions into plant communities.

~~**2.6. Modelling Plant Invasions**~~

~~Once an alien species has been introduced in sufficient numbers, its invasion success is contingent upon~~Studies on invasion success usually focus either on invasibility of the environment ~~and~~ or invasiveness of the species (Richardson & Pyšek 2006). In recent decades, more data has become available on regional differences in numbers of species invading, and species differences in invasion success. Together with data on environmental and socio-economic variables, species characteristics and introduction history, this information has revealed some general patterns providing insights into processes underlying plant invasions.

3.1. A Global Overview of the Naturalized Alien Flora

A recent compilation of >800 regional naturalized alien floras revealed that globally >13,000 plant species have become naturalized (van Kleunen et al. 2015a, Pyšek et al. 2017). In other words, ~4% of the extant vascular flora has expanded beyond species' native ranges with help of humans. Most of these naturalizations occurred in the last two centuries, and although the rate at which newly naturalized alien species are discovered has plateaued, it is not decreasing yet (Seebens et al. 2017). We can thus expect many more new naturalizations in the next decades, and a major research question is, how will they ~~will~~ be distributed around the globe ~~is one of the main questions~~ (**Figure 1**)?~~.~~

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North America has the highest number of naturalized plants, Antarctica has the lowest number, and the highest density occurs on the Pacific islands (van Kleunen et al. 2015a). The Northern Hemisphere continents are the major donors of naturalized species. Europe has even donated 288% more species than would be expected considering its small native flora (van

Kleunen et al. 2015a), probably as a consequence of European colonialism. Hotspots of plant invasions are found on islands and in coastal regions (Dawson et al. 2017, Pyšek et al. 2017). For mainland regions, naturalized plant species richness increases with decreasing mean annual temperature, and with increasing mean annual precipitation, human population density and per capita gross domestic product (Dawson et al. 2017). The importance of economic factors, specifically past bilateral trade, leads to the forecast that emerging economies, such as India and China, will see a rise in plant naturalizations in the next two decades (Seebens et al. 2015), and are also likely to become more important donors of naturalized species.

For invasive plants *sensu* Richardson et al. (2000)~~)(i.e., rapidly spreading alien plants~~; see section 2.1), few data on global patterns are currently available. A global analysis of invasive trees and shrubs showed, as for naturalized plants in general, that the highest numbers are found in North America and the Pacific Islands (Rejmánek & Richardson 2013). For invasive plants *sensu* CBD (2000)~~)(i.e., alien species threatening native biodiversity~~; see section 2.1), Pyšek et al. (2017) similarly showed that there is a strong correlation between the numbers of invasive and naturalized species in a region. Nevertheless, more data on invasive species *sensu* Richardson et al. (2000) and the different dimensions of invasiveness **(Figure 2)** are needed to better understand the global patterns and drivers of plant invasiveness.

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3.2. Propagule Pressure

Propagule pressure – a composite measure of the number of release events and the number of individuals released per event – is considered the most consistent driver of invasion success (Lockwood et al. 2005, 2007, Simberloff 2009). Theoretically, a high propagule pressure increases the likelihood of overcoming Allee effects, and demographic and environmental stochasticity (e.g., Shea & Possingham 2000). Empirical studies on propagule pressure of alien plants mostly use proxies such as sales or planting frequencies of ornamental plants (Dehnen-Schmutz et al. 2007, Feng et al. 2016, Maurel et al. 2016), and are correlative in nature. Introduction experiments, on the other hand, have the disadvantage that the~~y last~~ir duration is too short to capture the full invasion process. Nevertheless, the few available introduction experiments confirm that propagule pressure has a strong positive effect on early establishment of alien plants (e.g., Von Holle & Simberloff 2005, Kempel et al. 2013).

Despite the importance of propagule pressure, little is known about the roles of its elements. In theory, many released individuals per introduction event should help overcoming demographic stochasticity and Allee effects, whereas many introduction events should facilitate overcoming environmental stochasticity (Shea & Possingham 2000, Simberloff 2009). Experimental studies separating these propagule-pressure elements are rare and restricted to animals (e.g., Sinclair & Arnott 2016). Genetic variation, which is likely to increase with each additionally introduced individual, is another element of propagule pressure, and has been shown to play a role in *Spartina alterniflora* invasion in China (Wang et al. 2012). More experimental studies are needed that consider the roles of propagule pressure's different elements in alien plant invasions **(Figure 1)**, and also how they interact with other drivers.

3.3. Human disturbance

Disturbance by humans is thought to be another major driver of plant invasions (Lockwood et al. 2007). Disturbance is defined as any relatively discrete event in time that disrupts ecosystem, community or population structure, and changes resources, substrate availability or the physical environment (White & Pickett 1985). Many disturbances are naturally recurring events, and a change in disturbance regime by humans rather than the disturbance event itself may promote invasions (Hobbs & Huenneke 1992). This complexity makes generalizing across disturbance types difficult (Lockwood et al. 2007). Nevertheless, global (Dawson et al. 2017) and regional (e.g., McKinney 2001) analyses show that richness of naturalized and invasive plants are usually strongly associated with human-population density, which is ~~arguably a good surrogate for~~associated with human disturbance.

In a review, Colautti et al. (2006) showed that the majority of plant studies found that disturbance, usually involving the destruction of biomass, increases invasibility of plant communities. Most studies considered only invaders already in the system, which can obviously invade (Lockwood et al. 2007), and manipulated disturbances natural to the system. Recent experiments in which locally non-occurring species were introduced to native grassland communities showed that establishment from seed is considerably higher after tilling of the soil (i.e., a human disturbance; e.g., Kempel et al. 2013). Overall, there is thus good evidence that human disturbances promote biological invasions. However, which alien species benefit the most from disturbance and why, remains an open question (**Figure 1**).

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3.4. Responses to Additional Resources

Many disturbance events and anthropogenic global change drivers ~~may~~ change resource availabilities. As predicted by the fluctuating-resource-availability hypothesis (Davis et al. 2000), increases in resource availability make plant communities more susceptible to plant invasion (Seabloom et al. 2015). However, not all alien plants take advantage of increased resources; so successful alien plants may be those that capitalize most strongly on increased resources. ~~(Davidson et al. 2011) showed in a meta-analysis that invasive species were more plastic in growth, morphology and physiology than native species, but this did not result in fitness advantages. However, a~~A multi-species experiment showed that among native and among alien species in Switzerland, common species capitalized more on nutrient increases than rare species (Dawson et al. 2012a). Similarly, a meta-analysis showed that globally more widespread alien species exhibited greater biomass responses to increases in resources

(Dawson et al. 2012b). So, although some alien plants invade low-resource environments (Funk 2013), many invasive alien plants have a high capacity to capitalize on increased resource levels.

Environmental change is frequently characterized by a change in variability as well as in mean conditions. For example, floods and fires may temporarily increase nutrient availability. Parepa et al. (2013) showed that invasive *Fallopia* spp. grown with native plants benefited more strongly when supplied with nutrient pulses instead of a constant supply. In a multi-species experiment, naturalized alien plants produced more biomass when nutrients were provided as a single large pulse in the middle of the growth period compared to plants with a constant supply (Liu & van Kleunen 2017). The reverse was true for native plants. Thus, many successful alien plants are opportunists that take advantage of nutrient pulses. The underlying mechanisms still need more research (**Figure 1**).

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3.5. Lag Phases and Invasion Debts

Species need time to move from one invasion stage to the next. Once an alien plant has been introduced, there is a lag phase before it becomes ~~naturalizes~~naturalized, and one before it is considered to be ~~becomes~~ invasive (i.e., starts to accelerate its spread) (Crooks 2005). Unfortunately, few studies distinguish between the two lag phases, and no study quantified both. Lag phases may simply be an inherent characteristic of exponential population growth, or they may result from Allee effects or time needed for evolutionary adaptation or environmental change (Crooks 2005). A lack of hard data prevents us from understanding the importance of these mechanisms.

For ornamental and forestry species, the introduction-naturalization lag phase ranges from two to over 370 years (Kowarik 1995, Binggeli 2000, Caley et al. 2008, Daehler 2009). The few studies that quantified this lag phase indicate that it is shorter in tropical (Binggeli

2000, Daehler 2009) than in temperate (Kowarik 1995, Caley et al. 2008) regions, possibly because of year-round growth in the tropics (Daehler 2009). These studies further clearly show that shorter generation times result in shorter lag phases, suggesting that differences in lag phases may diminish if measured in terms of generation times.

The naturalization-invasion lag phase has been quantified using time series of herbarium records. Most of these lag phases are <50 years (Aikio et al. 2010, Larkin 2012). However, these lag phase estimates should be interpreted with caution as Hyndman et al. (2015) argued that several assumptions underlying the lag-phase-estimation approach were violated. For example, because the lag-phase estimation involves fitting models to cumulative numbers of herbarium records over time, the assumption of non-independence of the residuals is violated. Future studies on naturalization-invasion lag phases should aim to optimize statistical approaches, and then assess which factors drive variation in lag phases **(Figure 1)**.

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The existence of lag phases implies that the current numbers of naturalized and invasive alien species are determined by processes in the past. Indeed, Essl et al. (2011) demonstrated that current plant naturalization patterns in Europe are better explained by socioeconomic factors from the year 1900 than from the year 2000. Research on such so-called invasion debts (Seabloom et al. 2006) will thus be useful for predicting future invasions.

3.6. Climatic Suitability

Plant distributions have long been thought to be primarily restricted by biogeographic barriers and climatic conditions (Good 1931). Consequently, climatic suitability is considered a major predictor of plant invasion success (Panetta & Mitchell 1991). However, recently, several studies reported that ~40% (Guisan et al. 2014) or even >65% (Atwater et al. 2018) of invasive species have undergone climatic niche shifts. The reasons for these shifts require more research (**Figure 1**), but they~~,~~ call into queston~~ing~~ the assumption of climatic niche conservatism~~ into question~~. This suggests that estimates of climatic suitability from the native range may be poor predictors for invasion success. Surprisingly, few studies have explicitly related the modelled climatic suitability of introduced alien plants to their actual invasion success. The naturalization success of 449 Chinese woody species introduced to Europe was significantly correlated with climatic suitability (Feng et al. 2016). However, in that study, climatic suitability only explained 5% of the variance in naturalization success, possibly due to the large geographical extent (Europe) considered. On the other hand, a study on the garden flora of a small municipality in southern Germany found that climatic suitability was very strongly related to local naturalization success (Mayer et al. 2017). So, overall climatic suitability seems to be an important prerequisite for plant invasions.

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3.7. Species Characteristics

Baker (1965)'s list of 'ideal weed' characteristics was the starting point for research on species characteristics related to invasion success. Several reviews (Pyšek & Richardson 2007, van Kleunen et al. 2015b) and meta-analyses (van Kleunen et al. 2010b, Davidson et al. 2011) have summarized the results. Although some trends appear, results depend on whether invasive aliens are compared to natives or non-invasive~~-~~ aliens (van Kleunen et al. 2010b), and on the invasion stage considered (Dietz & Edwards 2006, Dawson et al. 2009). Nevertheless, a few characteristics are globally associated with naturalization success. Using a global database on breeding systems of 1752 plant species, Razanajatovo et al. (2016) showed that ~~species~~ with an increase in ~~greater~~ self-fertilization ability, the number of ~~were naturalized in more~~ regions around the world ~~globally~~in which a species is naturalized increased. Furthermore, species listed in databases ~~on~~as harmful invasive species (i.e., following the CBD (2000) definition of invasive; see section 2.1) are characterized by Small a small genome size and polyploidy are other plant characteristics globally associated with invasion success (Pandit et al. 2014). As genome size and polyploidy are no functional traits, we will need approaches such as path analysis to separate direct and indirect effects of functional traits associated with genomic characteristics on invasion success.

The general lack of consistent relationships between species characteristics and invasion success limits predictions of invasions based on those characteristics. This does not mean that species characteristics are unimportant. Predictive power may improve by considering invasion stage, invasiveness dimension, spatial scale and environmental context (van Kleunen et al. 2015b), by testing whether different species traits are associated with the different dimensions of invasiveness (**Figure 1**;, Catford et al. 2016). Studies also need to test for interactions between traits, and for non-linear relationships between invasion success and traits. Moreover, they should account for introduction bias, i.e., the phenomenon that species with certain characteristics were introduced earlier or more frequently, and consequently have higher apparent invasion success (Lockwood et al. 2005, Colautti et al. 2006, Maurel et al. 2016).

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3.8. The Way Forward for Research on General Patterns and Drivers of Invasion Success

Recently built databases describing the global distribution of naturalized and invasive alien plants allow researchers to address major macro-ecological questions on invasion success of alien plants. The geographical units for these databases are administrative regions of different sizes. Ideally, such data should include the habitat-affiliations within the regions, or should be collected for grid cellsgeo-referenced units of equal size. Another step forward would be to integrate the distributional data of naturalized alien and native species. This would allow assessing assessment of the importance of habitat filtering, and how much invasions contribute to homogenization of the global flora. Furthermore, to better understand the importance of species characteristics and historical factors in invasions, we need data on alien species that were introduced but failed to ~~establish~~naturalized (Dehnen-Schmutz et al. 2007, Maurel et al. 2016), at least until now. These data will also allow better quantification of invasion debt. Compilations of nursery catalogues and botanical garden inventories from around the world will be a good starting point for a global introduced alien flora.

A major objective of invasion biology is to understand the mechanisms driving invasion success, but studies on global patterns are correlative, not causative. Thus, some of the identified apparent drivers of plant invasion patterns might not be true drivers. For example, because propagule pressure is a major driver of invasion success, it should be ~~used as a null model~~ accounted for when testing the roles of e.g. species characteristics. However, it could be that the propagule pressure only appears to be important because species with characteristics that promote invasion success have been introduced more frequently (Maurel et al. 2016). Structural equation modelling (Shipley 2000) offers a potential statistical solution to better separate the direct and indirect drivers of plant invasions. Causative tests for generality of invasion drivers could further be achieved by establishing research networks that replicate experiments globally, similar to the Nutrient Network (http://www.nutnet.umn.edu/) and DroughtNet (http://wp.natsci.colostate.edu/droughtnet/) (Borer et al. 2014).

4. BIOTIC INTERACTIONS OF ALIEN PLANTS

Alien plants interact with native resident plants and other organisms. The resulting effects on alien plant performance and fitness determine whether a species is able to establish in a local community (Levine et al. 2004, MacDougall et al. 2009). Biotic interactions occur at the individual plant scale, but should affect invasion success at larger scales. For instance, altered biotic interactions in the introduced compared to the native range may modulate the realised niches of invasive plants in the introduced range, possibly leading to habitat expansion or climatic niche shifts (Guisan et al. 2014, Atwater et al. 2018).

4.1. Diversity of Resident Communities

Areas with high native species richness frequently also have high alien richness (Stohlgren et al. 2003). This likely results from habitat heterogeneity covarying with both native richness and alien richness at landscape scales (Levine et al. 2004). In contrast, at local scales – as predicted by Elton (1958)'s diversity-invasibility hypothesis – more species-rich communities are frequently more resistant to invasions (Levine et al. 2004). Most likely, this is because a more species-rich community occupies more of the available niche space. Although even the most diverse communities cannot resist invasions completely, there is strong support for the diversity-invasibility hypothesis (Levine et al. 2004). However, we still require studies involving communities not dominated by herbaceous species to assess the generality of the pattern, and studies testing the importance of phylogenetic and functional diversity to better understand the mechanisms underlying the pattern (**Figure 1**).

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4.2. Enemy Release

Alien plants may be released from herbivores and pathogens, especially from specialists that have not been co-introduced, resulting in a competitive advantage over natives. This so-called enemy-release hypothesis (Elton 1958, Keane & Crawley 2002) is perhaps the best known hypothesis in invasion ecology. Indeed, some invasive alien plants have fewer enemies associated with them and incur less damage in the introduced than in the native range (e.g., Mitchell & Power 2003, Meijer et al. 2016). However, results from studies comparing enemy damage on alien and co-occurring native species are equivocal, and many studies do not ~~link~~ assess how damage affects fitness of the ~~to~~ alien plant ~~performances~~ (Chun et al. 2010).

Most enemy-release studies focus on aboveground enemies, but the role of soil pathogens has gained attention (Dawson & Schrama 2016). Some European native plants invasive in North America grow better in sterilized than in non-sterilized soils, but only for ~~in~~ European soils, and ~~but~~ not ~~in~~ North American soils~~, after soil sterilisation~~ (Maron et al. 2014). This suggests that the European plants do not suffer from soil pathogens in North America. Such 'plant-soil-feedback' studies, however, treat soil as a black box. One exceptional example is a study on *Prunus serotina*, which in its native North American range suffers from high seedling mortality due to infection by specific oomycete pathogens, while in Europe these are less virulent (Reinhart et al. 2010). We need more such studies that verify which microbes have negative effects on plants and are absent in the introduced range.

Enemy release might decrease with time as enemies in the invaded range may shift hosts and start to utilise the invader (Diez et al. 2010). ~~There are reports, however, that some generalist soil pathogens that increased in abundance under invasive plants, spill over to~~ [illegible] However, new encounters at the expanding edges of invasions may also result in temporary enemy release, if the natural enemies there do not utilise the invader immediately. So, whether alien plants escape or recruit enemies at the range edges remains an open question [illegible] example, generalist soil pathogens ~~tha~~cant increase~~d~~ in abundance under invasive plants, spill over to infect native plants and thereby enhance invader dominance (e.g., *Chromolaena odorata* in India; Mangla et al. 2008). Therefore, the outcome of ~~these~~ novel encounters with enemies is ~~unknown~~~~hard~~difficult to predict for many alien plants.

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4.3. Novel Weapons

The novel weapons hypothesis posits that some chemical compounds of an alien species can negatively affect naïve native species (Callaway & Ridenour 2004). These novel weapons may be released as root exudates, or as leachates from living or dead plant material. The most famous example is the European plant *Centaurea stoebe*, which has allelopathic effects on native plants in the North American grasslands it invades, but not on competing plants in its native European range (Thorpe et al. 2009). The allelopathic effect of *C. stoebe* has been demonstrated in the field (Thorpe et al. 2009), but such field tests of the novel weapons hypothesis are rare.

Novel biochemistry may also have impacts on other organisms (Cappuccino & Arnason 2006). For example, novel defence chemicals may reduce herbivory by naïve herbivores (Macel et al. 2014), but there is no evidence that invasive alien plant are generally more deterrent to generalist herbivores than native plants are (Lind & Parker 2010). Some novel chemicals can also suppress mycorrhizal fungi beneficial to native competitors but not required by the invader, as shown for *Alliaria petiolata* in North America (Stinson et al. 2006). Over time, ~~the novelty of these weapons may wear off~~the native organisms may adapt to the novel chemicals (Lankau et al. 2009), but more research is needed to understand ~~ecological and evolutionary~~the processes involved. Another question that deserves research attention is whether ~~novelty of native plant~~ chemical compounds of native plants are novel to alien plants and contribute to ~~increases~~ resistance against invasion (**Figure 1**; Cummings et al. 2012).

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4.4. Mutualists

Mutualisms of plants with soil microbes, pollinators and seed dispersers may influence invasions, but have received less attention than enemies (Traveset & Richardson 2014).

Therefore, their relative importance remains unknown (**Figure 1**). Nitrogen-fixing microbes and mycorrhizal fungi are the two main groups of soil mutualists. Some ~~invasive~~ alien plants ~~have profited from~~are likely to have become invasive due to their ability of having nitrogen-fixing root symbionts, particularly when N-fixing is absent in the native ~~plant~~ species pool (Vitousek & Walker 1989). Alien plants may acquire the N-fixing microbes through co-introduction or 'ecological fitting' of alien plants to native N-~~fixers~~ fixing microbes (Le Roux et al. 2017), leading to shifts in N-fixer community composition between the native and alien ranges. ~~The latter is indicated by differences~~However, it is unclear if these shifts ~~in N-fixing rhizobial community composition between native and alien ranges of plants~~hinder or enhance [illegible]

As most plants have mycorrhizal fungal associations that help with the uptake of nutrients (Wang & Qiu 2006), invasion success may depend on mycorrhiza. Indeed, some tree invasions in South America depended upon the co-introduction of ectomycorrhizal fungi (Hayward et al. 2015). In Germany, mycorrhizal, and particularly facultative mycorrhizal, alien plants have a wider distribution than non-mycorrhizal species (Menzel et al. 2017). It is not yet known whether this relationship holds globally.

The vast majority of flowering plant species are pollinated by animals (Ollerton et al. 2011), but surprisingly few studies have explicitly assessed the importance of plant-pollinator mutualisms for plant invasions (Stout & Tiedeken 2017). Pollen limitation is relatively uncommon among invasive plants (Pyšek et al. 2011), possibly because of high ~~autofertility~~ self-fertilization ability (Razanajatovo et al. 2016) and ability to integrate in native plant-pollinator networks (Vilà et al. 2009). Surprisingly, Razanajatovo & van Kleunen (2016) found that non-naturalized alien species are also not pollen-limited. More studies are needed to test whether this is a general phenomenon. Few studies of plant-pollinator interactions (e.g., Stout et al. 2006) and ~~selfing~~ self-fertilization rates (e.g., Ollerton et al. 2012) have compared reproductive success in native and alien range populations. More sSuch studies would are needed to shed light onto whether shifts in pollinators or selfing self-fertilization in the alien range contribute to invasion success.

Alien plants are more likely to spread into (semi-)natural habitats if they recruit native fruit-consuming animals as seed dispersers (e.g., Cordeiro et al. 2004). However, the general importance of dispersal relative to other factors, and how plant-disperser dynamics change over time are still poorly understood. In aThe results of a study in rare dispersal experiment in Canada suggest that the invasive ant *Myrmica rubra*, as well as the native ant *Aphaenogaster rudis*, contribute to seed dispersal and thus spread of the invasive plant *Chelidonium majus*; the presence of a seed-dispersing invasive ant promoted dominance of invasive alien plants over natives (Prior et al. 2014). Introduced seed-dispersing animals can also facilitate invasions by alien plants in Hawai'IHawai'i, where fruits of *Myrica faya* are dispersed by the alien bird *Zosterops japonica* (Vitousek & Walker 1989). Thus currently non-naturalized plants may still pose a future invasion risk if a suitable disperser gets is subsequently introduced, leading to 'invasional meltdown' (Simberloff & Von Holle 1999).

4.5. The Way Forward for Research on Biotic Interactions of Alien Plants

Most research on biotic interactions as drivers determinants of alien plant success has focused on single interaction types, when in reality, multiple interactions occur simultaneously. There have been calls to consider multi-trophic interactions centred on alien plants (Harvey et al. 2010), though we have yet to move beyond the use of model interactors (often generalists) under greenhouse conditions (Kempel et al. 2013). While research on the role of plant-soil feedbacks in invasions is expanding, we often do not know which types of micro-organisms are the most important 'players' contributing to net soil-biota effects (Dawson & Schrama 2016). Progress here requires detailed studies that involve isolation, identification and re-inoculation of plants with putative soil pathogens and mutualists. We also recommend that more attention be paid to the role of mutualists of all types in invasions, in order to rebalance the current bias toward natural enemies.

Biotic interactions do not operate in a vacuum, and are contingent upon the traits and evolutionary history of both the alien plant and its putative interactors in the introduced range. Interactions may change over time as a result of ecological ~~or~~ and evolutionary processes. Thus, to better understand how biotic interactions have affected and will continue to affect invasions, we need to consider both evolutionary history, and current eco-evolutionary dynamics.

5. EVOLUTION AND GENETICS OF INVASIVE PLANTS

There is considerable potential for evolution resulting from plant introductions to new ranges. Alien plants ~~are less adapted to their new environments than to their native environments, they~~may experience novel conditions, and thus selection pressures, lack a history of coevolution with many interacting species, and may experience demographic bottlenecks or genomic admixture of distant ~~sources~~source populations. Thus, adaptive and random evolutionary processes are likely intensified in introduced populations, and our understanding of alien plants is incomplete without studying their genetics and evolution. Although this has long been recognised (Baker & Stebbins 1965, Brown & Marshall 1981), genetic and evolutionary studies of alien plants have increased only relatively recently (Bossdorf et al. 2005, Colautti & Lau 2015).

5.1. Phenotypic Evolution of Alien Plants

If introduced populations experience novel conditions, these will exert selection pressures on plant phenotypes that may result in rapid evolution, provided there is genetic variation.

Identifying phenotypic divergence between native and introduced populations requires approaches where offspring from different origins are grown in uniform environments, so that a genetic basis to phenotypic differences can be confirmed. In recent decades, there has been an explosion of common-garden studies with alien plants (reviewed in Bossdorf et al. 2005, Colautti et al. 2009, Felker-Quinn et al. 2013). These studies most often test the evolution of increased competitive ability (EICA) hypothesis, which proposes that some alien plants may have become invasive because of evolution~~ary shifts from~~ of reduced resource allocation to defenses and increased allocation to growth and reproduction (Blossey & Nötzold 1995). Some general patterns emerging from these studies are that (1) few studies found results that are completely in line with the predictions of ~~full support for~~ EICA ~~remains rare~~ (Felker-Quinn et al. 2013), but (2) significant differentiation often occurs in some growth or defense traits between native and introduced plant populations (Bossdorf et al. 2005, Colautti et al. 2009, Felker-Quinn et al. 2013, Colautti & Lau 2015). Thus, rapid phenotypic evolution appears to be common ~~in introduced plant populations~~after introductions of plant species into a new range.

Given the importance of herbivores and pathogens for plant evolution (Strauss & Zangerl 2002) and the often observed release from specialist enemies (Mitchell & Power 2003, Meijer et al. 2016), shifts in allocation of resources from specialist to generalist enemy defenses have been predicted in alien plants (shifting-defense hypothesis; Müller-Schärer et al. 2004). Feeding experiments and chemical analyses of common-garden plants confirmed that there are often differences in plant defenses between native and introduced populations, and that defenses ~~is~~ are reduced against specialists but not generalists (Doorduin & Vrieling 2011, Felker-Quinn et al. 2013). ~~-~~Full support for the shifting-defense hypothesis has been found in *Senecio jacobaea* where resistance to specialists is decreased but levels of ~~pyrrolizidine alkaloids and~~ defense against generalists are increased in introduced populations

(Joshi & Vrieling 2005). In most cases the results are more complex, with evolutionary changes in some aspects of defense but not others, shifts from constitutive to induced defenses, or *vice versa*, and often large geographic variation within introduced and native ranges (Orians & Ward 2010, Doorduin & Vrieling 2011, Felker-Quinn et al. 2013). However, when looking at the actual damage incurred by plants, a recent meta-analysis showed that while resistance against specialist herbivores decreased in introduced populations, resistance against generalist herbivores increased (Zhang et al. 2018). Taken together, the evidence indicates that defense traits are key targets of selection and are evolving rapidly in alien plants. This is also supported by experiments showing that exclusion of herbivores can indeed lead to strong evolutionary responses within few generations (e.g., Agrawal et al. 2012).

~~The common-garden approach has limitations that were sometimes overlooked in earlier studies.~~Many of the early studies on evolutionary change in invasive plants suffer from several weaknesses. Comparisons often involved low numbers of populations (Bossdorf et al. 2005), and some comparisons were less meaningful as they confounded introduced and native ranges with latitude or climate (Colautti et al. 2009). Comparisons were also often made without knowing the sources of introduction, which can be misleading particularly for species with one or few introductions. These pitfalls are now more widely recognized and accounted for. Recent studies have used molecular data to identify sources of introductions and then measured the phenotypic divergence between the source(s) and descendant populations (e.g., Liao et al. 2014).

Simple common-garden studies can provide evidence for evolution but not adaptation, and whether trait changes are really adaptive remains an open question (**Figure 1**). The latter requires reciprocal transplant experiments or the combination of experiments with selection measurements in wild populations. Both approaches are so far rare in the study of alien plants

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(Colautti & Lau 2015). A recent analysis of published selection coefficients suggests that on average, selection differentials are stronger in introduced than native populations, though data for introduced species were few (Colautti & Lau 2015). Moreover, very few studies tested for adaptive differentiation between ranges by transplanting plants between their native and introduced ranges, and the few that did (e.g., Maron et al. 2004, Williams et al. 2008) found little clear-cut evidence. All of these studies worked with only one or few sites per range, limiting their power to draw general conclusions.

More studies (reviewed in Colautti & Lau 2015, Oduor et al. 2016) reciprocally transplanted plants within the introduced range. Out of these studies, only one (Colautti & Barrett 2013) on *Lythrum salicaria* found local adaptation in all study sites, whereas others found ~~no or~~ only partial or no support for local adaptation. Nevertheless, a meta-analysis of ~~such~~ reciprocal transplant experiments within the introduced range of invasive species and within the native range of native species ~~the available evidence~~ indicates that adaptive evolutionary processes are at least as common and as strong in ~~in introduced plant populations as in native ones~~invasive as in native species (Oduor et al. 2016). This is surprising given that populations of invasive species had less time to adapt than populations of native species, and supports the idea of an increased rate of evolutionary change in invasive plants.

5.2. Evolutionary Impacts on Native Species

Alien plants can also cause evolutionary responses in native residents. In particular, invasive species are expected to exert selection on native species and cause evolutionary changes in invaded communities (Strauss et al. 2006). While evolutionary studies on alien plants initially focused entirely on alien evolution, recently attention has shifted toward evolutionary responses of native species. For instance, native plants growing together with spotted knapweed (*Centaurea maculosa*) in North America have evolved greater resistance to knapweed allelopathy (Callaway et al. 2005). A combination of selection analyses and reciprocal transplants in California showed that the exotic legume *Medicago polymorpha* alters selection and adaptation of the native *Lotus wrangelianus* (Lau 2006, 2008). Perhaps the most intriguing example of rapid evolution of a native species in response to an invasive plant is the coevolutionary dynamic between invasive *Alliaria petiolata* and native competitors in North America. It was shown that the level of the glucosinolate sinigrin rapidly evolves in invasive *Alliaria* populations in response to native competitors, but the native *Pilea pumila* equally rapidly evolves greater resistance to ~~these~~ this allelochemical~~s~~ (Lankau 2012). This could explain why glucosinolate concentrations decline with population age in *Alliaria* populations in North America (Lankau et al. 2009). Rapid evolution in response to invasive plants is common in native plants, as shown by a recent meta-analysis (Oduor 2013). Broadening evolutionary studies of alien plants to their native competitors and antagonists, and the coevolution between aliens and natives, is a promising and important area for future research **(Figure 1)**.

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5.3. Molecular Genetics of Invasions

In addition to traits, the ecology and evolution of alien plants has also been studied through molecular genetic analyses. Initially, these were mainly used for identifying pathways and numbers of introductions, and genetic bottlenecks (reviewed in Bossdorf et al. 2005, Dlugosch & Parker 2008). General insights from these studies are (1) contrary to expectations, genetic diversity is often only moderately reduced in introduced populations, (2) multiple introductions are common, and (3) admixture between different introductions can even increase genetic diversity in the introduced range. Since these earlier studies were usually done with neutral markers, they were often disconnected from trait-based studies. More recently, however, researchers have combined molecular with trait data, yielding more powerful evolutionary studies.

Molecular data can provide knowledge of introduction pathways, allowing ~~better matching of alien populations with native ones for comparison~~~~to choose~~ selection of the most likely native source populations as comparators for the invasive populations (e.g., Liao et al. 2014). One can also incorporate population structure and stochastic processes into trait analyses (Keller & Taylor 2008), analyse trait evolution along an invasion chronosequence (Barker et al. 2017), test for phenotypic consequences of population admixture (Keller & Taylor 2010), or compare specific hybrids or cytotypes of alien species (Hovick & Whitney 2014, Parepa et al. 2014).

Combining molecular and trait data can also ~~uncover~~ help to answer questions about the genetic basis of evolving traits, i.e., the genes or genomic regions associated with phenotypic changes in alien plants **(Figure 1)**. Recent advances in sequencing technologies allow high-resolution genomic data generation for any alien plant species, which can then be used to construct genetic maps for Quantitative Trait Loci (QTL) or genome-wide association studies. For example, Whitney et al. (2015) used a single-nucleotide-polymorphism map to identify QTLs underlying fitness variation in invasive sunflowers. Gould & Stinchcombe (2017) used whole-genome sequencing to show that flowering-time variation is associated with different genes in the introduced versus native range of *Arabidopsis thaliana*. The use of high-resolution genomic methods in invasion biology should be increased from now on.

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5.4. The Way Forward for Research on the Evolution and Genetics of Invasive Plants

Much progress has been made in studying alien plant genetics and evolution. Rapid trait evolution is common in aliens as well as their native neighbours, but support for the EICA hypothesis is limited. Common garden studies have limitations, and are unlikely to further our understanding of alien plant evolution on their own. Future evolutionary studies of alien plants should (1) study selection and adaptation in the native versus introduced range, (2) explore coevolution between alien and native species, and (3) make combinations of trait and molecular data the standard for more targeted and mechanistic evolution studies **(Figure 1)**.

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Most evolutionary studies of alien plants have been done on ~~contemporary individuals~~individuals representing the present generation of the populations rather than past generations, and were based on DNA sequence or trait data. However, two new research areas beyond these limits deserve mentioning, as they have the potential to greatly increase our understanding of alien plant evolution. First, with several hundred million specimens worldwide, herbaria represent huge historical archives of alien plant~~ evolutions~~s. DNA sequence variation of herbaria specimen can be analysed with standard methods (see Vandepitte et al. 2014~~)~~ for an example with alien plants) and with specific ancient DNA methods (Suchan et al. 2016). Future research should attempt to take more advantage of this treasure. Second, individuals of the same species can also differ epigenetically, and there is currently much speculation about the role of epigenetic processes in rapid adaptation (Richards et al. 2017). Recent studies on *Alternanthera philoxeroides* (Gao et al. 2010) and *Fallopia japonica* (Zhang et al. 2017) found that genetically identical populations in the introduced ranges are often epigenetically differentiated, and that epigenetic variation can be associated with environment or phenotype. The paucity of studies precludes general conclusions, but they suggest epigenetic variation may contribute to the invasion success of these species. This should motivate researchers to study this possibility more thoroughly in future.

6. CONCLUSIONS

In a time of rapid environmental and biotic change, understanding why certain alien species can successfully naturalize and become invasive has become a major objective in ecology and evolution. At the same time, because alien organisms experience novel ecological contexts, they provide study systems that advance our ecological and evolutionary understanding. The ecology and evolution of alien plants is a very broad field crossing different spatial and temporal scales, and with a plethora of hypotheses. We have highlighted some of the major conceptual and methodological advances, as well as empirical results, that we argue moved the field forward in the last decades or will do so in the near future. Although we did not discuss modelling approaches, there have also been major advances in developing more mechanistic models that bear great promise in predicting invasion risks (e.g., Carboni et al. 2018). We call for more transparency on which 'invasive' definition people use, and for a dissection of the different dimensions of invasiveness (**Figure 2**). Using the right comparators and accounting for introduction history may result in more consistent findings. By integrating modern theories on plant coexistence and applying phylogenetic and functional-trait approaches, by integrating mechanistic processes into modelling approaches, by studying the interplay between different biotic interactions, and by combining molecular with experimental evolutionary approaches, we will advance our understanding of alien plants and improve predictions on which aliens might invade in the future.

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Figure caption

Figure 1

Visual summary of research intensity, consistency of results and open questions in the study of alien plant ecology and evolution, including general patterns and drivers, biotic interactions, and the role of evolution and genetics. We use a four-level heat-colour scale for the different cells to indicate whether in our opinion, research intensity, consistency of results and open questions have low, moderate, high or very high values. With arrows, we indicate the trends (decreasing, continuing, increasing, rapidly increasing) in the rate of research on each topic. For each topic, we list our top question that needs to be answered to better understand the ecology and evolution of alien plants.

Figure 2

The stages and barriers (red bars) of the invasion process (after Richardson et al. 2000) and the multiple dimensions of invasiveness (e.g. Catford et al. 2016). When a species has been introduced from it native range across a biogeographic barrier it is an alien. Those aliens that passed the environmental barrier and are sometimes found in the wild but do not persist are casuals. ~~The ones~~Those that passed the environmental and reproductive barriers and thus form persistent populations are naturalized species. A subset of the naturalized aliens is considered invasive. Invasiveness, however, is not a binary variable but a continuous one and has multiple dimensions (i.e., distributional characteristics) indicated by the axes of the cube. Each of these invasiveness dimensions is associated with some main barrier along the continuum. Invasive species can theoretically occur anywhere within this multidimensional space. For example, species A is an invasive species that is a habitat specialist with a small range size that can become locally very abundant, due to overcoming competition from natives. Species B is an invasive species that has a large range through overcoming dispersal barriers, but is also a habitat specialist ~~but has a large range and~~with a low local abundance.

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Species C in an invasive species that has high values for each of the three invasiveness dimensions shown, and so has overcome competition, dispersal and environmental barriers.