

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, and the need for appropriate comparators while accounting for introduction history.

Developments in phylogenetic and functional-trait research, and hybrid modelling bear great promise. 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), and a lack of appropriate null models (Colautti et al. 2006) and comparator groups (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 topics where progress has been made, from macro-ecology and biotic interactions to evolution and genetics. Our review is

26 accompanied by a visual summary in **Figure 1** where we indicate, for each topic, how well it
27 has been studied so far, how consistent the results were and how many open questions there
28 still are in it. Although this figure is clearly somewhat subjective, we hope that together with
29 the ‘way-forward’ sections below, it will stimulate and guide future research on the ecology
30 and evolution of alien plants.

31

32 **2. CONCEPTUAL AND METHODOLOGICAL ADVANCES**

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

36

37 **2.1. The Invasion-stages Framework**

38 Invasion biology has developed a large vocabulary with multiple terms for the same things
39 (e.g., alien, exotic, non-native, non-indigenous), and multiple definitions for the same terms
40 (e.g., invasive; see below). To increase clarity and consistent use of terminology, Richardson
41 et al. (2000) proposed an invasion-stages framework with a sequence of barriers that a plant
42 species has to overcome to become invasive. In this framework, aliens are plant species that
43 have passed a biogeographic barrier (e.g., an ocean) with help of humans. The aliens that
44 have passed environmental and reproductive barriers, and have established wild populations
45 that persist over multiple life cycles, are considered naturalized. The naturalized species that
46 have overcome the dispersal barrier within the non-native range and subsequent
47 environmental barriers they encountered are considered invasive.

48 While the Richardson et al. framework is widely applied (3042 citations in Google
49 Scholar, accessed 11 January 2018), definitions of ‘invasive’ vary. The Richardson et al.

50 (2000) definition is neutral with respect to ecological and economic impacts, whereas the
51 Convention on Biological Diversity (CBD 2000) defines invasive species as those whose
52 introduction and/or spread threatens biological diversity. Problematic is that the latter is
53 frequently unknown. Other definitions of ‘invasive’ are used less frequently, although they
54 consider interesting aspects. For example, (Alpert et al. 2000) proposed decoupling ‘invasive’
55 from being alien, and Hufbauer & Torchin (2007) proposed defining a species invasive when
56 its demographic performance is higher in the invaded than in the native range. While many
57 alien species might qualify as invasive under all these definitions, there are exceptions.
58 Parker et al. (2013) showed that plants among ‘*100 of the world’s worst invasive alien*
59 *species*’, which follows the CBD (2000) definition, perform on average better in their non-
60 native than in their native ranges, thus meeting the Hufbauer & Torchin (2007) ‘invasive’
61 definition. However, there was high variability among these species in this regard. Although
62 none of the ‘invasive’ definitions is necessarily better than the others, the use of multiple
63 definitions has resulted in confusion, and might explain some of the apparently conflicting
64 findings among studies. Therefore, we call for researchers to always state clearly which
65 definition of ‘invasive’ is used. Here, we use the Richardson et al. (2000) definitions of alien,
66 naturalized and invasive.

67

68 **2.2. The Multiple Dimensions of Invasiveness**

69 The multiple ‘invasive’ definitions demonstrate that invasive species are not a homogeneous
70 group. While some alien species are locally abundant, they might have a small non-native
71 range or be restricted to few habitats, whereas others might have a large range and occur in
72 many habitats but have sparse populations. The idea that rarity and commonness have three
73 dimensions – geographical range, habitat specificity, local population size – was originally
74 developed by Rabinowitz (1981), but has only recently been applied to invasiveness of alien

75 plants (Dawson et al. 2013, Catford et al. 2016). Potential additional dimensions of
76 invasiveness are spread rate (Catford et al. 2016), and different categories of ecological and
77 economic impacts. We believe that consideration of these different invasiveness dimensions
78 in research on alien plants may provide more consistent results among studies.

79

80 **2.3. Comparative Approaches for Assessing Determinants of Invasion Success**

81 The variety in approaches used to study alien plants and their invasion success is enormous.
82 While there are many descriptive studies on invasive species, the question what determines
83 invasion success requires a comparative approach. Such studies are most powerful when they
84 include many species, populations and sites (van Kleunen et al. 2014). The comparator choice
85 is pivotal to whether the question of interest can be answered (van Kleunen et al. 2010a).
86 Although most studies on traits associated with invasiveness have compared invasive alien to
87 native species (Pyšek & Richardson 2007, van Kleunen et al. 2010b, Davidson et al. 2011),
88 this cannot reveal why alien species differ in invasiveness. This requires a comparison
89 between invasive and non-invasive alien species, though it is also important to realize that the
90 latter may be at different invasion stages. Some non-invasive aliens might not have been
91 introduced, and others might be introduced but not naturalized (van Kleunen et al. 2015b). As
92 different traits might be associated with each of these stages (Dietz & Edwards 2006, Dawson
93 et al. 2009, van Kleunen et al. 2015b), the results of the comparison between invasive and
94 non-invasive aliens may strongly depend on the invasion stage of the latter.

95

96 **2.4. Introduction History as a Null Model**

97 It seems almost trivial that alien species introduced in greater numbers or more frequently are
98 more likely to naturalise and become invasive, and thus should be accounted for.

99 Nevertheless, this so-called propagule pressure has been formalized as a ‘null model’ for
100 invasion success only recently (Colautti et al. 2006). Similarly, alien species that were
101 introduced earlier should have had more opportunities to naturalize and become invasive
102 (Rejmánek 2000). We will discuss the importance of propagule pressure and year of
103 introduction in more detail below. However, accounting for the introduction history of an
104 alien species has been important for disentangling the ecological and evolutionary processes
105 that contribute to plant invasions.

106

107 **2.5. Darwin’s Naturalization Conundrum, Scale Dependency and Coexistence Theory**

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

119 The realization that different ecological processes act at different spatial scales is
120 helping to resolve this conundrum and the mixed findings (Thuiller et al. 2010). Whereas
121 abiotic environmental filtering, which requires pre-adaptation, acts at all spatial scales, biotic
122 filtering acts only at the small scales where species interact (Thuiller et al. 2010, Gallien &
123 Carboni 2016). Therefore, Darwin’s naturalization hypothesis should only operate at small

124 spatial scales. As the different processes might act simultaneously, the relationship between
125 invasion success and phylogenetic distance might actually be non-linear and depend on the
126 phylogenetic scale (Thuiller et al. 2010, Gallien & Carboni 2016).

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

138

139 **2.6. Modelling Plant Invasions**

140 Modelling approaches are essential for forecasting plant invasions. Species-distribution
141 models relate a species' occurrences to environmental variables (Guisan & Zimmermann
142 2000), and allow forecasting of potential ranges for large numbers of alien species. These
143 phenomenological models have the limitation that they do not explicitly consider biotic
144 interactions and assume that species distributions are in equilibrium with their environment
145 (Guisan & Zimmermann 2000). Moreover, they do not consider demographic processes (e.g.,
146 dispersal, germination, growth, survival, reproduction), which are central to understanding
147 invasions (Gurevitch et al. 2011). Mechanistic or process-based models do not have these
148 limitations, but can be very data demanding (Gallien et al. 2010). Higgins & Richardson

149 (2014) partly overcame this by calibrating a mechanistic model using species distribution
150 data for 749 Australian acacia and eucalypt trees. The model correctly predicted 92% of the
151 occurrences elsewhere in the world, and showed that invasion success is associated with
152 physiological tolerance.

153 Recently, there have been major advances in linking both types of models using
154 hybrid models (e.g., Dullinger et al. 2012) and dynamic-range models (Pagel & Schurr 2012).
155 Furthermore, a hierarchical Bayesian modelling approach has been developed whereby a
156 meta-model estimates species presences, constrained by the results of multiple sub-models
157 (Talluto et al. 2016). Integrated approaches have also been developed for dynamic modelling
158 of plant-functional groups to forecast changes in the vegetation and the biodiversity in a
159 landscape over time (Boulangéat et al. 2014). These mechanistic modelling approaches are
160 now starting to be used to predict plant invasions. For example, Carboni et al. (2018) used a
161 hybrid dynamic-vegetation model to forecast invasion risk in a mountain area under different
162 scenarios of changes in climate, land-use and propagule pressure. Increases in computational
163 power and the rapid development of modelling approaches will further advance our ability to
164 robustly predict plant invasions.

165

166 **3. GENERAL PATTERNS AND DRIVERS OF INVASION SUCCESS**

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

174

175 **3.1. A Global Overview of the Naturalized Alien Flora**

176 A recent compilation of >800 regional naturalized alien floras revealed that globally >13,000
177 plant species have become naturalized (van Kleunen et al. 2015a, Pyšek et al. 2017). In other
178 words, ~4% of the extant vascular flora has expanded beyond species' native ranges with
179 help of humans. Most of these naturalizations occurred in the last two centuries, and although
180 the rate at which newly naturalized alien species are discovered has plateaued, it is not
181 decreasing yet (Seebens et al. 2017). We can thus expect many more new naturalizations in
182 the next decades.

183 North America has the highest number of naturalized plants, Antarctica has the lowest
184 number, and the highest density occurs on the Pacific islands (van Kleunen et al. 2015a). The
185 Northern Hemisphere continents are the major donors of naturalized species. Europe has even
186 donated 288% more species than would be expected considering its small native flora (van
187 Kleunen et al. 2015a), probably as a consequence of European colonialism. Hotspots of plant
188 invasions are found on islands and in coastal regions (Dawson et al. 2017, Pyšek et al. 2017).
189 For mainland regions, naturalized plant species richness increases with decreasing mean
190 annual temperature, and with increasing mean annual precipitation, human population density
191 and per capita gross domestic product (Dawson et al. 2017). The importance of economic
192 factors, specifically past bilateral trade, leads to the forecast that emerging economies, such
193 as India and China, will see a rise in plant naturalizations in the next two decades (Seebens et
194 al. 2015).

195 For invasive plants *sensu* Richardson et al. (2000)(i.e., rapidly spreading alien plants),
196 few data on global patterns are currently available. A global analysis of invasive trees and
197 shrubs showed, as for naturalized plants in general, that the highest numbers are found in
198 North America and the Pacific Islands (Rejmánek & Richardson 2013). For invasive plants

199 *sensu* CBD (2000)(i.e., alien species threatening native biodiversity), Pyšek et al. (2017)
200 similarly showed that there is a strong correlation between the numbers of invasive and
201 naturalized species in a region. Nevertheless, more data on invasive species *sensu* Richardson
202 et al. (2000) are needed to better understand the global patterns and drivers of plant
203 invasiveness.

204

205 **3.2. Propagule Pressure**

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

217 Despite the importance of propagule pressure, little is known about the roles of its
218 elements. In theory, many released individuals per introduction event should help
219 overcoming demographic stochasticity and Allee effects, whereas many introduction events
220 should facilitate overcoming environmental stochasticity (Shea & Possingham 2000,
221 Simberloff 2009). Experimental studies separating these propagule-pressure elements are rare
222 and restricted to animals (e.g., Sinclair & Arnott 2016). Genetic variation, is another element
223 of propagule pressure, and has been shown to play a role in *Spartina alterniflora* invasion in

224 China (Wang et al. 2012). More experimental studies are needed that consider the roles of
225 propagule pressure's different elements in alien plant invasions, and also how they interact
226 with other drivers.

227

228 **3.3. Human disturbance**

229 Disturbance is thought to be another major driver of plant invasions (Lockwood et al. 2007).

230 Disturbance is defined as any relatively discrete event in time that disrupts ecosystem,

231 community or population structure, and changes resources, substrate availability or the

232 physical environment (White & Pickett 1985). Many disturbances are naturally recurring

233 events, and a change in disturbance regime rather than the disturbance event itself may

234 promote invasions (Hobbs & Huenneke 1992). This complexity makes generalizing across

235 disturbance types difficult (Lockwood et al. 2007). Nevertheless, global (Dawson et al. 2017)

236 and regional (e.g., McKinney 2001) analyses show that richness of naturalized and invasive

237 plants are usually strongly associated with human-population density, which is arguably a

238 good surrogate for human disturbance.

239 In a review, Colautti et al. (2006) showed that the majority of plant studies found that

240 disturbance increases invasibility of plant communities. Most studies considered only

241 invaders already in the system, which can obviously invade (Lockwood et al. 2007), and

242 manipulated disturbances natural to the system. Recent experiments in which locally non-

243 occurring species were introduced to native grassland communities showed that

244 establishment from seed is considerably higher after tilling of the soil (i.e., a human

245 disturbance; e.g., Kempel et al. 2013). Overall, there is thus good evidence that human

246 disturbances promote biological invasions.

247 **3.4. Responses to Additional Resources**

248 Many disturbance events and anthropogenic global change drivers may change resource
249 availabilities. As predicted by the fluctuating-resource-availability hypothesis (Davis et al.
250 2000), increases in resource availability make plant communities more susceptible to plant
251 invasion (Seabloom et al. 2015). However, not all alien plants take advantage of increased
252 resources; so successful alien plants may be those that capitalize most strongly on increased
253 resources. (Davidson et al. 2011) showed in a meta-analysis that invasive species were more
254 plastic in growth, morphology and physiology than native species, but this did not result in
255 fitness advantages. However, a multi-species experiment showed that among native and
256 among alien species in Switzerland, common species capitalized more on nutrient increases
257 than rare species (Dawson et al. 2012a). Similarly, a meta-analysis showed that globally more
258 widespread alien species exhibited greater biomass responses to increases in resources
259 (Dawson et al. 2012b). So, although some alien plants invade low-resource environments
260 (Funk 2013), many invasive alien plants have a high capacity to capitalize on increased
261 resource levels.

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

270

271 **3.5. Lag Phases and Invasion Debts**

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

279 For ornamental and forestry species, the introduction-naturalization lag phase ranges
280 from two to over 370 years (Kowarik 1995, Binggeli 2000, Caley et al. 2008, Daehler 2009).
281 The few studies that quantified this lag phase indicate that it is shorter in tropical (Binggeli
282 2000, Daehler 2009) than in temperate (Kowarik 1995, Caley et al. 2008) regions, possibly
283 because of year-round growth in the tropics (Daehler 2009). These studies further clearly
284 show that shorter generation times result in shorter lag phases, suggesting that differences in
285 lag phases may diminish if measured in terms of generation times.

286 The naturalization-invasion lag phase has been quantified using time series of
287 herbarium records. Most of these lag phases are <50 years (Aikio et al. 2010, Larkin 2012).
288 However, these lag phase estimates should be interpreted with caution as Hyndman et al.
289 (2015) argued that assumptions underlying the lag-phase-estimation approach were violated.
290 Future studies on naturalization-invasion lag phases should aim to optimize statistical
291 approaches, and then assess which factors drive variation in lag phases.

292 The existence of lag phases implies that the current numbers of naturalized and
293 invasive alien species are determined by processes in the past. Indeed, Essl et al. (2011)
294 demonstrated that current plant naturalization patterns in Europe are better explained by
295 socioeconomic factors from the year 1900 than from the year 2000. Research on such so-

296 called invasion debts (Seabloom et al. 2006) will thus be useful for predicting future
297 invasions.

298

299 **3.6. Climatic Suitability**

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

315

316 **3.7. Species Characteristics**

317 Baker (1965)'s list of 'ideal weed' characteristics was the starting point for research on
318 species characteristics related to invasion success. Several reviews (Pyšek & Richardson
319 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 greater self-fertilization ability were naturalized in more regions
globally. 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, 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).

340

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 to address major macro-ecological questions on invasion success of alien plants.

345 The geographical units for these databases are administrative regions of different sizes.
346 Ideally, such data should include the habitat-affiliations within the regions, or should be
347 collected for grid cells. Another step forward would be to integrate the distributional data of
348 naturalized alien and native species. This would allow assessing the importance of habitat
349 filtering, and how much invasions contribute to homogenization of the global flora.
350 Furthermore, to better understand the importance of species characteristics and historical
351 factors in invasions, we need data on alien species that were introduced but failed to
352 establish, at least until now. These data will also allow better quantification of invasion debt.
353 Compilations of nursery catalogues and botanical garden inventories will be a good starting
354 point for a global introduced alien flora.

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

367

368 **4. BIOTIC INTERACTIONS OF ALIEN PLANTS**

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

376

377 **4.1. Diversity of Resident Communities**

378 Areas with high native species richness frequently also have high alien richness (Stohlgren et
379 al. 2003). This likely results from habitat heterogeneity covarying with both native richness
380 and alien richness at landscape scales (Levine et al. 2004). In contrast, at local scales – as
381 predicted by Elton (1958)’s diversity-invasibility hypothesis – more species-rich
382 communities are frequently more resistant to invasions (Levine et al. 2004). Most likely, this
383 is because a more species-rich community occupies more of the available niche space.

384 Although even the most diverse communities cannot resist invasions completely, there is
385 strong support for the diversity-invasibility hypothesis (Levine et al. 2004). However, we still
386 require studies involving communities not dominated by herbaceous species, and studies
387 testing the importance of phylogenetic and functional diversity.

388

389 **4.2. Enemy Release**

390 Alien plants may be released from herbivores and pathogens, especially from specialists,
391 resulting in a competitive advantage over natives. This so-called enemy-release hypothesis

392 (Elton 1958, Keane & Crawley 2002) is perhaps the best known hypothesis in invasion
393 ecology. Indeed, some invasive alien plants have fewer enemies associated with them and
394 incur less damage in the introduced than in the native range (e.g., Mitchell & Power 2003,
395 Meijer et al. 2016). However, results from studies comparing enemy damage on alien and co-
396 occurring native species are equivocal, and many studies do not link damage to alien plant
397 performance (Chun et al. 2010).

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

408 Enemy release might decrease with time as enemies in the invaded range may shift
409 hosts and utilise the invader (Diez et al. 2010). There are reports, however, that some
410 generalist soil pathogens that increased in abundance under invasive plants, spill over to
411 infect native plants and thereby enhance invader dominance (e.g., *Chromolaena odorata* in
412 India; Mangla et al. 2008). Some invasive species have even acquired pathogens that have so
413 far never been identified on native species (e.g., *Microstegium vimineum* in eastern North
414 America; Stricker et al. 2016). Alien plants should acquire more new enemies with time since
415 introduction and range expansion. However, new encounters at the expanding edges of

416 invasions may also result in temporary enemy release, if the natural enemies there do not
417 utilise the invader. The outcome of these novel encounters is unknown for many alien plants.

418

419 **4.3. Novel Weapons**

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

428 Novel biochemistry may also have impacts on other organisms (Cappuccino &
429 Arnason 2006). For example, novel defence chemicals may reduce herbivory by naïve
430 herbivores (Macel et al. 2014), but there is no evidence that invasive alien plant are generally
431 more deterrent to generalist herbivores than native plants are (Lind & Parker 2010). Some
432 novel chemicals can also suppress mycorrhizal fungi beneficial to native competitors but not
433 required by the invader, as shown for *Alliaria petiolata* in North America (Stinson et al.
434 2006). Over time, the novelty of these weapons may wear off (Lankau et al. 2009), but more
435 research is needed to understand ecological and evolutionary processes involved. Another
436 question that deserves research attention is whether novelty of native plant chemical
437 compounds increases resistance against invasion (Cummings et al. 2012).

438

439 **4.4. Mutualists**

440 Mutualisms of plants with soil microbes, pollinators and seed dispersers may influence
441 invasions, but have received less attention than enemies (Traveset & Richardson 2014).
442 Nitrogen-fixing microbes and mycorrhizal fungi are the two main groups of soil mutualists.
443 Some invasive plants have profited from nitrogen-fixing root symbionts, particularly when N-
444 fixing is absent in the native plant species pool (Vitousek & Walker 1989). Alien plants may
445 acquire the N-fixing microbes through co-introduction or ‘ecological fitting’ of alien plants to
446 native N-fixers (Le Roux et al. 2017). The latter is indicated by differences in N-fixing
447 rhizobial community composition between native and alien ranges of plants (e.g., in
448 *Trifolium*; Shelby et al. 2016). Currently, however, we lack a more general understanding of
449 the importance of rhizobial community changes to invasion success of the alien plants.

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

456 The vast majority of flowering plant species are pollinated by animals (Ollerton et al.
457 2011), but surprisingly few studies have explicitly assessed the importance of plant-pollinator
458 mutualisms for plant invasions (Stout & Tiedeken 2017). Pollen limitation is relatively
459 uncommon among invasive plants (Pyšek et al. 2011), possibly because of high autofertility
460 (Razanajatovo et al. 2016) and ability to integrate in native plant-pollinator networks (Vilà et
461 al. 2009). Surprisingly, Razanajatovo & van Kleunen (2016) found that non-naturalized alien
462 species are also not pollen-limited. More studies are needed to test whether this is a general
463 phenomenon. Few studies of plant-pollinator interactions (e.g., Stout et al. 2006) and selfing

464 rates (e.g., Ollerton et al. 2012) have compared reproductive success in native and alien range
465 populations. Such studies would shed light onto whether shifts in pollinators or selfing in the
466 alien range contribute to invasion success.

467 Alien plants are more likely to spread into (semi-)natural habitats if they recruit native
468 fruit-consuming animals as seed dispersers (e.g., Cordeiro et al. 2004). However, the general
469 importance of dispersal relative to other factors, and how plant-disperser dynamics change
470 over time are still poorly understood. In a rare dispersal experiment in Canada, the presence
471 of a seed-dispersing invasive ant promoted dominance of invasive alien plants over natives
472 (Prior et al. 2014). Introduced seed-dispersing animals can also facilitate invasions by alien
473 plants in Hawai’I, where fruits of *Myrica faya* are dispersed by the alien bird *Zosterops*
474 *japonica* (Vitousek & Walker 1989). Thus currently non-naturalized plants may still pose a
475 future invasion risk if a suitable disperser gets introduced, leading to ‘invasional meltdown’
476 (Simberloff & Von Holle 1999).

477

478 **4.5. The Way Forward for Research on Biotic Interactions of Alien Plants**

479 Most research on biotic interactions as drivers of alien plant success has focused on single
480 interaction types, when in reality, multiple interactions occur simultaneously. There have
481 been calls to consider multi-trophic interactions centred on alien plants (Harvey et al. 2010),
482 though we have yet to move beyond the use of model interactors (often generalists) under
483 greenhouse conditions (Kempel et al. 2013). While research on the role of plant-soil
484 feedbacks in invasions is expanding, we often do not know which types of micro-organisms
485 are the most important ‘players’ contributing to net soil-biota effects (Dawson & Schrama
486 2016). Progress here requires detailed studies that involve isolation, identification and re-
487 inoculation of plants with putative soil pathogens and mutualists. We also recommend that

488 more attention be paid to the role of mutualists of all types in invasions, in order to rebalance
489 the current bias toward natural enemies.

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

496

497 **5. EVOLUTION AND GENETICS OF INVASIVE PLANTS**

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

507

508 **5.1. Phenotypic Evolution of Alien Plants**

509 If introduced populations experience novel conditions, these will exert selection pressures on
510 plant phenotypes that may result in rapid evolution. Identifying phenotypic divergence
511 between native and introduced populations requires approaches where offspring from

512 different origins are grown in uniform environments, so that a genetic basis to phenotypic
513 differences can be confirmed. In recent decades, there has been an explosion of common-
514 garden studies with alien plants (reviewed in Bossdorf et al. 2005, Colautti et al. 2009,
515 Felker-Quinn et al. 2013). These studies most often test the evolution of increased
516 competitive ability (EICA) hypothesis, which proposes that some alien plants may have
517 become invasive because of evolutionary shifts from defenses to growth and reproduction
518 (Blossey & Nötzold 1995). Some general patterns emerging from these studies are that (1)
519 full support for EICA remains rare (Felker-Quinn et al. 2013), but (2) significant
520 differentiation often occurs in some growth or defense traits between native and introduced
521 plant populations (Bossdorf et al. 2005, Colautti et al. 2009, Felker-Quinn et al. 2013,
522 Colautti & Lau 2015). Thus, rapid phenotypic evolution appears to be common in introduced
523 plant populations.

524 Given the importance of herbivores and pathogens for plant evolution (Strauss &
525 Zangerl 2002) and the often observed release from specialist enemies (Mitchell & Power
526 2003, Meijer et al. 2016), shifts from specialist to generalist enemy defense have been
527 predicted in alien plants (shifting-defense hypothesis; Müller-Schärer et al. 2004). Feeding
528 experiments and chemical analyses of common-garden plants confirmed that there are often
529 differences in plant defense between native and introduced populations, and that defense is
530 reduced against specialists but not generalists (Doorduyn & Vrieling 2011, Felker-Quinn et al.
531 2013). Full support for the shifting-defense hypothesis has been found in *Senecio jacobaea*
532 where resistance to specialists is decreased but levels of pyrrolizidine alkaloids and defense
533 against generalists are increased in introduced populations (Joshi & Vrieling 2005). In most
534 cases the results are more complex, with evolutionary changes in some aspects of defense but
535 not others, shifts from constitutive to induced defenses, or *vice versa*, and often large
536 geographic variation within ranges (Orrians & Ward 2010, Doorduyn & Vrieling 2011, Felker-

537 Quinn et al. 2013). Taken together, the evidence indicates that defense traits are key targets of
538 selection and are evolving rapidly in alien plants. This is supported by experiments showing
539 that exclusion of herbivores can indeed lead to strong evolutionary responses within few
540 generations (e.g., Agrawal et al. 2012).

541 The common-garden approach has limitations that were sometimes overlooked in
542 earlier studies. Comparisons often involved low numbers of populations (Bossdorf et al.
543 2005), and some comparisons were less meaningful as they confounded range with latitude or
544 climate (Colautti et al. 2009). Comparisons were also often made without knowing the
545 sources of introduction, which can be misleading particularly for species with one or few
546 introductions. These pitfalls are now more widely recognized and accounted for. Recent
547 studies have used molecular data to identify sources of introductions and then measured the
548 phenotypic divergence between the source(s) and descendant populations (e.g., Liao et al.
549 2014).

550 Simple common-garden studies can provide evidence for evolution but not adaptation.
551 The latter requires reciprocal transplant experiments or the combination of experiments with
552 selection measurements in wild populations. Both approaches are so far rare in the study of
553 alien plants (Colautti & Lau 2015). A recent analysis of published selection coefficients
554 suggests that on average, selection differentials are stronger in introduced than native
555 populations, though data for introduced species were few (Colautti & Lau 2015). Moreover,
556 very few studies tested for adaptive differentiation between ranges by transplanting plants
557 between their native and introduced ranges, and the few that did (e.g., Maron et al. 2004,
558 Williams et al. 2008) found little clear-cut evidence. All of these studies worked with only
559 one or few sites per range, limiting their power to draw general conclusions. More studies
560 (reviewed in Colautti & Lau 2015) reciprocally transplanted plants within the introduced
561 range. Out of these studies, only one (Colautti & Barrett 2013) on *Lythrum salicaria* found

562 local adaptation in all study sites, whereas others found no or only partial support for local
563 adaptation. Nevertheless, the available evidence indicates that adaptive evolutionary
564 processes are common and as strong in introduced plant populations as in native ones (Oduor
565 et al. 2016).

566

567 **5.2. Evolutionary Impacts on Native Species**

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

587

588 **5.3. Molecular Genetics of Invasions**

589 In addition to traits, the evolution of alien plants has also been studied through molecular
590 genetic analyses. Initially, these were mainly used for identifying pathways and numbers of
591 introductions, and genetic bottlenecks (reviewed in Bossdorf et al. 2005, Dlugosch & Parker
592 2008). General insights from these studies are (1) contrary to expectations, genetic diversity
593 is often only moderately reduced in introduced populations, (2) multiple introductions are
594 common, and (3) admixture between different introductions can even increase genetic
595 diversity. Since these earlier studies were usually done with neutral markers, they were often
596 disconnected from trait-based studies. More recently, however, researchers have combined
597 molecular with trait data, yielding more powerful evolutionary studies.

598 Molecular data can provide knowledge of introduction pathways, allowing better
599 matching of alien populations with native ones for comparison (e.g., Liao et al. 2014). One
600 can also incorporate population structure and stochastic processes into trait analyses (Keller
601 & Taylor 2008), analyse trait evolution along an invasion chronosequence (Barker et al.
602 2017), test for phenotypic consequences of population admixture (Keller & Taylor 2010), or
603 compare specific hybrids or cytotypes of alien species (Hovick & Whitney 2014, Parepa et al.
604 2014).

605 Combining molecular and trait data can also uncover the genetic basis of evolving
606 traits, i.e., the genes or genomic regions associated with phenotypic changes in alien plants .
607 Recent advances in sequencing technologies allow high-resolution genomic data generation
608 for any alien plant species, which can then be used to construct genetic maps for Quantitative
609 Trait Loci (QTL) or genome-wide association studies. For example, Whitney et al. (2015)
610 used a single-nucleotide-polymorphism map to identify QTLs underlying fitness variation in

611 invasive sunflowers. Gould & Stinchcombe (2017) used whole-genome sequencing to show
612 that flowering-time variation is associated with different genes in the introduced versus native
613 range of *Arabidopsis thaliana*. The use of high-resolution genomic methods in invasion
614 biology should be increased from now on.

615

616 **5.4. The Way Forward for Research on the Evolution and Genetics of Invasive Plants**

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

624 Most evolutionary studies of alien plants have been done on contemporary
625 individuals, and were based on DNA sequence or trait data. However, two new research areas
626 beyond these limits deserve mentioning, as they have the potential to greatly increase our
627 understanding of alien plant evolution. First, with several hundred million specimens
628 worldwide, herbaria represent huge historical archives of alien plant evolution. DNA
629 sequence variation of herbaria specimen can be analysed with standard methods (see
630 Vandepitte et al. 2014) for example with alien plants) and with specific ancient DNA
631 methods (Suchan et al. 2016). Future research should attempt to take more advantage of this
632 treasure. Second, individuals of the same species can also differ epigenetically, and there is
633 currently much speculation about the role of epigenetic processes in rapid adaptation
634 (Richards et al. 2017). Recent studies on *Alternanthera philoxeroides* (Gao et al. 2010) and
635 *Fallopia japonica* (Zhang et al. 2017) found that genetically identical populations in the

636 introduced ranges are often epigenetically differentiated, and that epigenetic variation can be
637 associated with environment or phenotype. The paucity of studies precludes general
638 conclusions, but they suggest epigenetic variation may contribute to the invasion success of
639 these species. This should motivate researchers to study this possibility more thoroughly in
640 future.

641

642 **6. CONCLUSIONS**

643 In a time of rapid environmental and biotic change, understanding why certain alien species
644 can successfully naturalize and become invasive has become a major objective in ecology
645 and evolution. At the same time, because alien organisms experience novel ecological
646 contexts, they provide study systems that advance our ecological and evolutionary
647 understanding. The ecology and evolution of alien plants is a very broad field crossing
648 different spatial and temporal scales, and with a plethora of hypotheses. We have highlighted
649 some of the major conceptual and methodological advances, as well as empirical results, that
650 we argue moved the field forward in the last decades or will do so in the near future. We call
651 for more transparency on which ‘invasive’ definition people use, and for a dissection of the
652 different dimensions of invasiveness. Using the right comparators and accounting for
653 introduction history may result in more consistent findings. By integrating modern theories
654 on plant coexistence and applying phylogenetic and functional-trait approaches, by
655 integrating mechanistic processes into modelling approaches, by studying the interplay
656 between different biotic interactions, and by combining molecular with experimental
657 evolutionary approaches, we will advance our understanding of alien plants and improve
658 predictions on which aliens might invade in the future.

659

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663

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668

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1048 **Figure caption**

1049

1050 **Figure 1**

1051 Visual summary of research intensity, consistency of results and open questions in the study of alien
1052 plant ecology and evolution, including general patterns and drivers, biotic interactions, and the role of
1053 evolution and genetics. We use a four-level heat-colour scale for the different cells to indicate whether
1054 in our opinion, research intensity, consistency of results and open questions have low, moderate, high
1055 or very high values. With arrows, we indicate the trends (decreasing, continuing, increasing, rapidly
1056 increasing) in the rate of research on each topic. For each topic, we list our top question that needs to
1057 be answered to better understand the ecology and evolution of alien plants.

1058

		Research intensity	Consistency of results	Open questions	Top question
General patterns and drivers	3.1 Global overview	↑	High/moderate	High/moderate	What will be the future global distribution of alien plants?
	3.2 Propagule pressure	→	Very high/many	High/moderate	How important are the different elements of propagule pressure?
	3.3 Human disturbance	→	High/moderate	Low/few	Which alien species benefit from disturbance, and why?
	3.4 Additional resources	↗	High/moderate	High/moderate	What mechanisms allow invasive plants to benefit from resource pulses?
	3.5 Lag phases	↘	Low/few	High/moderate	What explains the existence and length of lag phases?
	3.6 Climatic suitability	→	High/moderate	Low/few	What drives climatic niche shifts in the alien range?
	3.7 Species characteristics	→	Very high/many	High/moderate	Are different species traits associated with each invasiveness dimension?
Biotic interactions	4.1 Diversity of residents	→	Very high/many	High/moderate	How important are phylogenetic and functional diversity?
	4.2 Enemy release	→	Low/few	High/moderate	Do alien plants escape or recruit enemies at the range edges?
	4.3 Novel weapons	↘	High/moderate	Low/few	Do natives have novel weapons to resist alien invaders?
	4.4 Mutualists	↗	Low/few	Very high/many	How important are mutualists compared to antagonists in driving invasions?
Genetics and evolution	5.1 Phenotypic evolution	→	Low/few	High/moderate	Are trait changes in introduced populations really adaptive?
	5.2 Evolutionary impacts	→	Low/few	Very high/many	How frequent is rapid coevolution of aliens and natives?
	5.3 Molecular genetics	→	High/moderate	High/moderate	What is the genetic basis of observed phenotypic evolution?

Intensity, consistency/questions

- Low/few
- Moderate
- High/many
- Very high/many

Rate of research intensity

- ↑ Rapidly increasing
- ↗ Increasing
- Continuing
- ↘ Decreasing