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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 twofold: 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

26 do not provide a systematic, exhaustive review, but ~~a series of~~ rather an overview of selected
27 key topics where progress has been made, from macro-ecology and biotic interactions to
28 evolution and genetics. Our review is accompanied by a visual summary in **Figure 1** where
29 we indicate, for each topic, how well it has been studied so far, how consistent the results
30 ~~were and how many open questions there still are in it~~ have been from study to study, and how
31 many questions remain open. Although this figure is clearly somewhat subjective, we hope
32 that together with the ‘way-forward’ sections below, it will stimulate and guide future
33 research on the ecology and evolution of alien plants.

34

35 **2. CONCEPTUAL AND METHODOLOGICAL ADVANCES**

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

39

40 **2.1. The Invasion-stages Framework**

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

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

55 While the Richardson et al. framework is widely applied (3042 citations in Google
56 Scholar, accessed 11 January 2018), definitions of ‘invasive’ vary. The Richardson et al.
57 (2000) definition is neutral with respect to ecological and economic impacts, whereas the
58 Convention on Biological Diversity (CBD 2000) defines invasive species as those whose
59 introduction and/or spread threatens biological diversity. Problematic is that the latter is
60 frequently unknown. Other definitions of ‘invasive’ are used less frequently, although they
61 consider interesting aspects. For example, [Alpert et al. \(2000\)](#) proposed decoupling
62 ‘invasive’ from being alien, and [Hufbauer & Torchin \(2007\)](#) proposed defining a species
63 invasive when its demographic performance is higher in the invaded than in the native range.
64 While many alien species might qualify as invasive under all these definitions, there are
65 exceptions. [Parker et al. \(2013\)](#) showed that plants among ‘*100 of the world’s worst invasive*
66 *alien species*’, which follows the CBD (2000) definition, perform on average better in their
67 non-native than in their native ranges, thus meeting the [Hufbauer & Torchin \(2007\)](#)
68 ‘invasive’ definition. However, there was high variability among these species in this regard.
69 Although none of the ‘invasive’ definitions is necessarily better than the others, the use of
70 multiple definitions has resulted in confusion, and might explain some of the apparently
71 conflicting findings among studies. Therefore, we call for researchers to always state clearly
72 which definition of ‘invasive’ is used. Here, we use the Richardson et al. (2000) definitions of
73 alien, naturalized and invasive, [unless stated otherwise](#).

74

75 **2.2. The Multiple Dimensions of Invasiveness**

76 ~~The multiple ‘invasive’ definitions demonstrate that i~~Invasive species, as described in the
77 ~~literature,~~ are not a homogeneous group. ~~While the Richardson et al. (2000) definition of~~
78 ~~invasive primarily focuses on spread of the naturalized species, it also implicitly also~~
79 ~~assumes that the species are locally abundant (i.e., produce reproductive offspring in large~~
80 ~~numbers). Species show continuous variation in spread (i.e., range size) and abundance,~~
81 ~~and which means that invasiveness is not binary, but is instead therefore a continuous~~
82 ~~variable and multidimensional, rather than a binary (yes/no) variable. Moreover, w~~While
83 some ~~naturalized~~ alien species are ~~wide-spread, they have a low locally abundant abundance,~~
84 ~~they might have a small non-native range or be restricted to few habitats,~~ whereas others
85 might have a ~~large-small~~ range and ~~occur in many habitats but have sparse populations~~ have a
86 ~~high local abundance. In other words, invasiveness has multiple dimensions (Figure 2). For~~ **Formatted: Font: Bold**
87 ~~the related concept of The idea that rarity and commonness (or rarity), Rabinowitz (1981)~~
88 ~~proposed, have three dimensions – in addition to geographical range, and habitat specificity,~~
89 local population size (i.e., abundance), to also consider the range of habitats in which a
90 ~~species occurs (i.e., habitat generality). This idea of multiple dimensions of a species’~~
91 ~~distribution or commonness, — was originally developed by Rabinowitz (1981), but has only~~
92 recently been applied to invasiveness of alien plants (Dawson et al. 2013, Catford et al.
93 2016).

94 The different invasiveness dimensions are likely to be associated with different main **Formatted: Indent: First line: 1.27 cm**
95 barriers (Figure 2). Range size (spread) may be mainly determined by one or more dispersal **Formatted: Font: Bold**
96 barriers, local abundance by one or more competition barriers, and habitat generality by one
97 or more environmental barriers. Depending on the specific research question, one could also
98 consider~~Potential additional further~~ dimensions, such as ~~of invasiveness are the rate of~~
99 spread~~rate~~ (Catford et al. 2016), and different categories of ecological and economic impacts.

100 which would then also include the CBD (2000) definition of invasive. We believe that
101 consideration of these different invasiveness dimensions in research on alien plants may
102 provide more consistent results among studies~~prevent researchers from mistakenly~~
103 concluding that results are in conflict.
104

105 **2.3. Comparative Approaches for Assessing Determinants of Invasion Success**

106 The variety in approaches used to study alien plants and their invasion success is enormous.
107 While there are many descriptive studies on individual invasive species, the question of what
108 determines invasion success requires a comparative approach. Such studies are most powerful
109 when they include many species, populations and sites (van Kleunen et al. 2014). The
110 comparator choice is pivotal to whether the question of interest can be answered (van
111 Kleunen et al. 2010a). Although most studies on traits associated with invasiveness have
112 compared invasive alien to native species (Pyšek & Richardson 2007, van Kleunen et al.
113 2010b, Davidson et al. 2011), this cannot reveal why alien species differ in invasiveness. This
114 requires a comparison between alien species that differ in their degree of
115 invasiveness~~between invasive and non-invasive alien species, either along a single dimension~~
116 or along multiple dimensions of the invasiveness continuum (Figure 2). When these
117 comparisons include non-invasive alien species, ~~though~~ it is also important to realize that
118 the latter may be at different invasion stages. ~~Some non-invasive aliens; some might not be~~
119 not found outside of cultivation, some are just casuals and others are naturalized but not
120 invasive~~have been introduced, and others might be introduced but not naturalized (van~~
121 Kleunen et al. 2015b**Figure 2**). As different traits might be associated with each of these
122 stages (Dietz & Edwards 2006, Dawson et al. 2009, van Kleunen et al. 2015b), the results of
123 the comparison between invasive and non-invasive aliens may strongly depend on the
124 invasion stage of the latter.

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125

126 **2.4. ~~Introduction History as a Null Model~~ Accounting for propagule pressure and year**
127 **of introduction**

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

130 Nevertheless, the need to account for this so-called propagule pressure has been ~~formalized as~~
131 ~~a 'null model' for invasion success~~ recognized only recently (Colautti et al. 2006). Similarly,
132 alien species that were introduced earlier should have had more opportunities to naturalize
133 and become invasive (Rejmánek 2000). We will discuss the importance of propagule pressure
134 and year of introduction in more detail below. However, accounting for ~~the introduction~~
135 ~~history~~ propagule pressure and year of introduction of ~~an~~ alien species has been important for
136 disentangling the ecological and evolutionary processes that contribute to plant invasions.

137

138 **2.5. Darwin's Naturalization Conundrum, Scale Dependency and Coexistence Theory**

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

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

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

175

176 **2.6. Modelling Plant Invasions**

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

185

186 **3.1. A Global Overview of the Naturalized Alien Flora**

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

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

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

207 For invasive plants *sensu* Richardson et al. (2000) ~~(i.e., rapidly spreading alien plants;~~
208 [see section 2.1](#)), few data on global patterns are currently available. A global analysis of
209 invasive trees and shrubs showed, as for naturalized plants in general, that the highest
210 numbers are found in North America and the Pacific Islands (Rejmánek & Richardson 2013).

211 For invasive plants *sensu* CBD (2000) ~~(i.e., alien species threatening native biodiversity; see~~
212 [section 2.1](#)), Pyšek et al. (2017) similarly showed that there is a strong correlation between
213 the numbers of invasive and naturalized species in a region. Nevertheless, more data on
214 invasive species *sensu* Richardson et al. (2000) [and the different dimensions of invasiveness](#)
215 [\(Figure 2\)](#) are needed to better understand the global patterns and drivers of plant
216 invasiveness.

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218 **3.2. Propagule Pressure**

219 Propagule pressure – a composite measure of the number of release events and the number of
220 individuals released per event – is considered the most consistent driver of invasion success
221 (Lockwood et al. 2005, 2007, Simberloff 2009). Theoretically, a high propagule pressure
222 increases the likelihood of overcoming Allee effects, and demographic and environmental
223 stochasticity (e.g., Shea & Possingham 2000). Empirical studies on propagule pressure of

224 alien plants mostly use proxies such as sales or planting frequencies of ornamental plants
225 (Dehnen-Schmutz et al. 2007, Feng et al. 2016, Maurel et al. 2016), and are correlative in
226 nature. Introduction experiments, on the other hand, have the disadvantage that ~~they last~~
227 [duration is](#) too short to capture the full invasion process. Nevertheless, the few available
228 introduction experiments confirm that propagule pressure has a strong positive effect on early
229 establishment of alien plants (e.g., Von Holle & Simberloff 2005, Kempel et al. 2013).

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

241

242 **3.3. Human disturbance**

243 Disturbance [by humans](#) is thought to be another major driver of plant invasions (Lockwood et
244 al. 2007). Disturbance is defined as any relatively discrete event in time that disrupts
245 ecosystem, community or population structure, and changes resources, substrate availability
246 or the physical environment (White & Pickett 1985). Many disturbances are naturally
247 recurring events, and a change in disturbance regime [by humans](#) rather than the disturbance
248 event itself may promote invasions (Hobbs & Huenneke 1992). This complexity makes

249 generalizing across disturbance types difficult (Lockwood et al. 2007). Nevertheless, global
250 (Dawson et al. 2017) and regional (e.g., McKinney 2001) analyses show that richness of
251 naturalized and invasive plants are usually strongly associated with human-population
252 density, which is ~~arguably a good surrogate for~~associated with human disturbance.

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

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262 **3.4. Responses to Additional Resources**

263 Many disturbance events and anthropogenic global change drivers ~~may~~ change resource
264 availabilities. As predicted by the fluctuating-resource-availability hypothesis (Davis et al.
265 2000), increases in resource availability make plant communities more susceptible to plant
266 invasion (Seabloom et al. 2015). However, not all alien plants take advantage of increased
267 resources; so successful alien plants may be those that capitalize most strongly on increased
268 resources. ~~(Davidson et al. 2011) showed in a meta-analysis that invasive species were more~~
269 ~~plastic in growth, morphology and physiology than native species, but this did not result in~~
270 ~~fitness advantages. However, a~~ multi-species experiment showed that among native and
271 among alien species in Switzerland, common species capitalized more on nutrient increases
272 than rare species (Dawson et al. 2012a). Similarly, a meta-analysis showed that globally more
273 widespread alien species exhibited greater biomass responses to increases in resources

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

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

285 [The underlying mechanisms still need more research \(Figure 1\).](#)

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287 3.5. Lag Phases and Invasion Debts

288 Species need time to move from one invasion stage to the next. Once an alien plant has been
289 introduced, there is a lag phase before it ~~becomes naturalizes~~naturalized, and one before it ~~is~~
290 ~~considered to be~~ ~~becomes~~-invasive (~~i.e., starts to accelerate its spread~~) (Crooks 2005).

291 Unfortunately, few studies distinguish between the two lag phases, and no study quantified
292 both. Lag phases may simply be an inherent characteristic of exponential population growth,
293 or they may result from Allee effects or time needed for evolutionary adaptation or
294 environmental change (Crooks 2005). A lack of hard data prevents us from understanding the
295 importance of these mechanisms.

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

299 2000, Daehler 2009) than in temperate (Kowarik 1995, Caley et al. 2008) regions, possibly
300 because of year-round growth in the tropics (Daehler 2009). These studies further clearly
301 show that shorter generation times result in shorter lag phases, suggesting that differences in
302 lag phases may diminish if measured in terms of generation times.

303 The naturalization-invasion lag phase has been quantified using time series of
304 herbarium records. Most of these lag phases are <50 years (Aikio et al. 2010, Larkin 2012).
305 However, these lag phase estimates should be interpreted with caution as Hyndman et al.
306 (2015) argued that [several](#) assumptions underlying the lag-phase-estimation approach were
307 violated. [For example, because the lag-phase estimation involves fitting models to cumulative](#)
308 [numbers of herbarium records over time, the assumption of non-independence of the](#)
309 [residuals is violated.](#) Future studies on naturalization-invasion lag phases should aim to
310 optimize statistical approaches, and then assess which factors drive variation in lag phases
311 [\(Figure 1\).](#)

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

318

319 **3.6. Climatic Suitability**

320 Plant distributions have long been thought to be primarily restricted by biogeographic barriers
321 and climatic conditions (Good 1931). Consequently, climatic suitability is considered a major
322 predictor of plant invasion success (Panetta & Mitchell 1991). However, recently, several
323 studies reported that ~40% (Guisan et al. 2014) or even >65% (Atwater et al. 2018) of

324 invasive species have undergone climatic niche shifts. The reasons for these shifts require
325 more research (Figure 1), but they call into question the assumption of climatic niche
326 conservatism ~~into question~~. This suggests that estimates of climatic suitability from the native
327 range may be poor predictors for invasion success. Surprisingly, few studies have explicitly
328 related the modelled climatic suitability of introduced alien plants to their actual invasion
329 success. The naturalization success of 449 Chinese woody species introduced to Europe was
330 significantly correlated with climatic suitability (Feng et al. 2016). However, in that study,
331 climatic suitability only explained 5% of the variance in naturalization success, possibly due
332 to the large geographical extent (Europe) considered. On the other hand, a study on the
333 garden flora of a small municipality in southern Germany found that climatic suitability was
334 very strongly related to local naturalization success (Mayer et al. 2017). So, overall climatic
335 suitability seems to be an important prerequisite for plant invasions.

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337 3.7. Species Characteristics

338 Baker (1965)'s list of 'ideal weed' characteristics was the starting point for research on
339 species characteristics related to invasion success. Several reviews (Pyšek & Richardson
340 2007, van Kleunen et al. 2015b) and meta-analyses (van Kleunen et al. 2010b, Davidson et al.
341 2011) have summarized the results. Although some trends appear, results depend on whether
342 invasive aliens are compared to natives or non-invasive aliens (van Kleunen et al. 2010b),
343 and on the invasion stage considered (Dietz & Edwards 2006, Dawson et al. 2009).
344 Nevertheless, a few characteristics are globally associated with naturalization success. Using
345 a global database on breeding systems of 1752 plant species, Razanajatovo et al. (2016)
346 showed that species with an increase in greater self-fertilization ability, the number of
347 naturalized in more regions around the world globally in which a species is naturalized
348 increased. Furthermore, species listed in databases as harmful invasive species (i.e.,

349 following the CBD (2000) definition of invasive; see section 2.1) are characterized by ~~Small~~ a small
350 genome size and polyploidy are ~~highly~~ traits globally associated with invasion success (Pardoll et al. 2014). As genome size and polyploidy are
351 functional traits, we ~~will~~ need approaches such as path analysis to separate direct and indirect
352 effects of functional traits associated with genomic characteristics on invasion success.

353 The general lack of consistent relationships between species characteristics and
354 invasion success limits predictions of invasions based on those characteristics. This does not
355 mean that species characteristics are unimportant. Predictive power may improve by
356 considering invasion stage, ~~invasiveness dimension~~, spatial scale and environmental context
357 (van Kleunen et al. 2015b), by testing whether different species traits are associated with the
358 different dimensions of invasiveness (Figure 1; Catford et al. 2016). Studies also need to test
359 for interactions between traits, and for non-linear relationships between invasion success and
360 traits. Moreover, they should account for introduction bias, i.e., the phenomenon that species
361 with certain characteristics were introduced earlier or more frequently, and consequently have
362 higher apparent invasion success (Lockwood et al. 2005, Colautti et al. 2006, Maurel et al.
363 2016).

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365 **3.8. The Way Forward for Research on General Patterns and Drivers of Invasion**

366 **Success**

367 Recently built databases describing the global distribution of naturalized and invasive alien
368 plants allow researchers to address major macro-ecological questions on invasion success of
369 alien plants. The geographical units for these databases are administrative regions of different
370 sizes. Ideally, such data should include the habitat-affiliations within the regions, or should be
371 collected for grid cells/geo-referenced units of equal size. Another step forward would be to
372 integrate the distributional data of naturalized alien and native species. This would allow
373 assessing/assessment of the importance of habitat filtering, and how much invasions

374 contribute to homogenization of the global flora. Furthermore, to better understand the
375 importance of species characteristics and historical factors in invasions, we need data on alien
376 species that were introduced but failed to ~~establish~~ [naturalized \(Dehnen-Schmutz et al. 2007,](#)
377 [Maurel et al. 2016\)](#), at least until now. These data will also allow better quantification of
378 invasion debt. Compilations of nursery catalogues and botanical garden inventories [from](#)
379 [around the world](#) will be a good starting point for a global introduced alien flora.

380 A major objective of invasion biology is to understand the mechanisms driving
381 invasion success, but studies on global patterns are correlative, not causative. Thus, some of
382 the identified apparent drivers of plant invasion patterns might not be true drivers. For
383 example, because propagule pressure is a major driver of invasion success, it should be ~~used~~
384 [as a null model accounted for](#) when testing the roles of e.g. species characteristics. However,
385 it could be that the propagule pressure only appears to be important because species with
386 characteristics that promote invasion success have been introduced more frequently (Maurel
387 et al. 2016). Structural equation modelling (Shipley 2000) offers a [potential](#) statistical
388 solution to better separate the direct and indirect drivers of plant invasions. Causative tests for
389 generality of invasion drivers could further be achieved by establishing research networks
390 ~~that require only~~ [in the Native Network \(www.nativeinvasions.org\) and the Global Invasive Species Database \(GISD\) \(Bochet 2014\)](#)

391

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

393 Alien plants interact with native resident plants and other organisms. The resulting effects on
394 alien plant performance and fitness determine whether a species is able to establish in a local
395 community (Levine et al. 2004, MacDougall et al. 2009). Biotic interactions occur at the
396 individual plant scale, but should affect invasion success at larger scales. For instance, altered
397 biotic interactions in the introduced compared to the native range may modulate the realised

398 niches of invasive plants in the introduced range, possibly leading to habitat expansion or
399 climatic niche shifts (Guisan et al. 2014, Atwater et al. 2018).

400

401 **4.1. Diversity of Resident Communities**

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

408 Although even the most diverse communities cannot resist invasions completely, there is
409 strong support for the diversity-invasibility hypothesis (Levine et al. 2004). However, we still
410 require studies involving communities not dominated by herbaceous species [to assess the](#)
411 [generality of the pattern](#), and studies testing the importance of phylogenetic and functional
412 diversity [to better understand the mechanisms underlying the pattern \(Figure 1\).](#)

413

414 **4.2. Enemy Release**

415 Alien plants may be released from herbivores and pathogens, especially from specialists [that](#)
416 [have not been co-introduced](#), resulting in a competitive advantage over natives. This so-called
417 enemy-release hypothesis (Elton 1958, Keane & Crawley 2002) is perhaps the best known
418 hypothesis in invasion ecology. Indeed, some invasive alien plants have fewer enemies
419 associated with them and incur less damage in the introduced than in the native range (e.g.,
420 Mitchell & Power 2003, Meijer et al. 2016). However, results from studies comparing enemy

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421 damage on alien and co-occurring native species are equivocal, and many studies do not
422 ~~link assess how~~ damage affects fitness of the ~~to~~ alien plant ~~performances~~ (Chun et al. 2010).

423 Most enemy-release studies focus on aboveground enemies, but the role of soil
424 pathogens has gained attention (Dawson & Schrama 2016). Some European native plants
425 invasive in North America grow better in sterilized than in non-sterilized soils, but only for
426 European soils, and ~~but not in~~ North American soils, ~~after soil sterilisation~~ (Maron et al.
427 2014). This suggests that the European plants do not suffer from soil pathogens in North
428 America. Such ‘plant-soil-feedback’ studies, however, treat soil as a black box. One
429 exceptional example is a study on *Prunus serotina*, which in its native North American range
430 suffers from high seedling mortality due to infection by specific oomycete pathogens, while
431 in Europe these are less virulent (Reinhart et al. 2010). We need more such studies that verify
432 which microbes have negative effects on plants and are absent in the introduced range.

433 Enemy release might decrease with time as enemies in the invaded range may shift
434 hosts and start to utilise the invader (Diez et al. 2010). ~~There are reports, however, that some~~
435 ~~generalist soil pathogens that increased in abundance under invasive plants, spill over to~~
436 ~~native plants (e.g., *Chromolaena odorata* in India; Mangla et al. 2008). Therefore, the outcome of these novel encounters with~~
437 However, new encounters at the expanding edges of invasions may also result in temporary
438 enemy release, if the natural enemies there do not utilise the invader immediately. So,
439 whether alien plants escape or recruit enemies at the range edges remains an open question
440 (Fridlind et al. 2010; Muth et al. 2011). However, new encounters at the expanding edges of invasions may also result in temporary
441 example, generalist soil pathogens that can't increased in abundance under invasive plants, spill
442 over to infect native plants and thereby enhance invader dominance (e.g., *Chromolaena*
443 *odorata* in India; Mangla et al. 2008). Therefore, the outcome of these novel encounters with
444 enemies is unknown ~~hard~~ difficult to predict for many alien plants.

Commented [WD1]: I think elsewhere we use ‘alien’ rather than ‘introduced’, but either way, I guess we should be consistent.

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446 **4.3. Novel Weapons**

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

455 Novel biochemistry may also have impacts on other organisms (Cappuccino &
456 Arnason 2006). For example, novel defence chemicals may reduce herbivory by naïve
457 herbivores (Macel et al. 2014), but there is no evidence that invasive alien plant are generally
458 more deterrent to generalist herbivores than native plants are (Lind & Parker 2010). Some
459 novel chemicals can also suppress mycorrhizal fungi beneficial to native competitors but not
460 required by the invader, as shown for *Alliaria petiolata* in North America (Stinson et al.
461 2006). Over time, ~~the novelty of these weapons may wear off~~the native organisms may adapt
462 to the novel chemicals (Lankau et al. 2009), but more research is needed to understand
463 ~~ecological and evolutionary~~the processes involved. Another question that deserves research
464 attention is whether ~~novelty of native plant~~ chemical compounds of native plants are novel to
465 alien plants and contribute to increases resistance against invasion (**Figure 1**; Cummings et
466 al. 2012).

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467

468 **4.4. Mutualists**

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

471 Therefore, their relative importance remains unknown (Figure 1). Nitrogen-fixing microbes
472 and mycorrhizal fungi are the two main groups of soil mutualists. Some invasive-alien plants
473 have profited from are likely to have become invasive due to their ability of having nitrogen-
474 fixing root symbionts, particularly when N-fixing is absent in the native plant-species pool
475 (Vitousek & Walker 1989). Alien plants may acquire the N-fixing microbes through co-
476 introduction or 'ecological fitting' of alien plants to native N-fixers-fixing microbes (Le Roux
477 et al. 2017), leading to shifts in N-fixer community composition between the native and alien
478 ranges. The latter is indicated by differences However, it is unclear if these shifts in N-fixing
479 rhizobial community composition between native and alien ranges of plants hinder or enhance
480 invasion (Stout et al. 2006) and the effect of nitrogen-fixing microbes on plant invasion is unclear

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

487 The vast majority of flowering plant species are pollinated by animals (Ollerton et al.
488 2011), but surprisingly few studies have explicitly assessed the importance of plant-pollinator
489 mutualisms for plant invasions (Stout & Tiedeken 2017). Pollen limitation is relatively
490 uncommon among invasive plants (Pyšek et al. 2011), possibly because of high autofertility
491 self-fertilization ability (Razanajatovo et al. 2016) and ability to integrate in native plant-
492 pollinator networks (Vilà et al. 2009). Surprisingly, Razanajatovo & van Kleunen (2016)
493 found that non-naturalized alien species are also not pollen-limited. More studies are needed
494 to test whether this is a general phenomenon. Few studies of plant-pollinator interactions
495 (e.g., Stout et al. 2006) and selfing-self-fertilization rates (e.g., Ollerton et al. 2012) have

496 compared reproductive success in native and alien range populations. [More s](#)Such studies ~~would are~~
497 [needed to](#) shed light onto whether shifts in pollinators or [selfing-self-fertilization](#) in the alien range
498 contribute to invasion success.

499 Alien plants are more likely to spread into (semi-)natural habitats if they recruit native
500 fruit-consuming animals as seed dispersers (e.g., Cordeiro et al. 2004). However, the general
501 importance of dispersal relative to other factors, and how plant-disperser dynamics change
502 over time are still poorly understood. ~~In a~~The results of a study in ~~are~~ dispersal experiment in Canada [suggest that the](#)
503 [invasive ant *Myrmica rubra*, as well as the native ant *Aphaenogaster rudis*, contribute to seed](#)
504 [dispersal of *Carduus marianus* in a field experiment](#) ~~in a field experiment in Canada~~ (Pitt 2014)
505 Introduced seed-dispersing animals ~~can~~ also facilitate invasions by alien plants in ~~Hawai~~^{Hawai}ⁱ, where
506 fruits of *Myrica faya* are dispersed by the alien bird *Zosterops japonica* (Vitousek & Walker
507 1989). Thus currently non-naturalized plants may still pose a future invasion risk if a suitable
508 disperser ~~gets is subsequently~~ introduced, ~~leading to 'invasional meltdown'~~ (Simberloff & Von Holle 1999).
509

510 **4.5. The Way Forward for Research on Biotic Interactions of Alien Plants**

511 Most research on biotic interactions as [drivers-determinants](#) of alien plant success has focused
512 on single interaction types, when in reality, multiple interactions occur simultaneously. There
513 have been calls to consider multi-trophic interactions centred on alien plants (Harvey et al.
514 2010), though we have yet to move beyond the use of model interactors (often generalists)
515 under greenhouse conditions (Kempel et al. 2013). While research on the role of plant-soil
516 feedbacks in invasions is expanding, we often do not know which types of micro-organisms
517 are the most important 'players' contributing to net soil-biota effects (Dawson & Schrama
518 2016). Progress here requires detailed studies that involve isolation, identification and re-
519 inoculation of plants with putative soil pathogens and mutualists. We also recommend that

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

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

528

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

530 There is considerable potential for evolution resulting from plant introductions to new ranges.

531 Alien plants ~~are less adapted to their new environments than to their native environments,~~
532 ~~they may experience novel conditions, and thus selection pressures,~~ lack a history of
533 coevolution with many interacting species, and may experience demographic bottlenecks or
534 genomic admixture of distant ~~sources~~ source populations. Thus, adaptive and random
535 evolutionary processes are likely intensified in introduced populations, and our understanding
536 of alien plants is incomplete without studying their genetics and evolution. Although this has
537 long been recognised (Baker & Stebbins 1965, Brown & Marshall 1981), genetic and
538 evolutionary studies of alien plants have increased only relatively recently (Bossdorf et al.
539 2005, Colautti & Lau 2015).

540

541 **5.1. Phenotypic Evolution of Alien Plants**

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

544 Identifying phenotypic divergence between native and introduced populations requires
545 approaches where offspring from different origins are grown in uniform environments, so
546 that a genetic basis to phenotypic differences can be confirmed. In recent decades, there has
547 been an explosion of common-garden studies with alien plants (reviewed in Bossdorf et al.
548 2005, Colautti et al. 2009, Felker-Quinn et al. 2013). These studies most often test the
549 evolution of increased competitive ability (EICA) hypothesis, which proposes that some alien
550 plants may have become invasive because of evolutionary shifts from of reduced resource
551 allocation to defenses and increased allocation to growth and reproduction (Blossey &
552 Nötzold 1995). Some general patterns emerging from these studies are that (1) few studies
553 found results that are completely in line with the predictions of full support for EICA remains
554 rare (Felker-Quinn et al. 2013), but (2) significant differentiation often occurs in some growth
555 or defense traits between native and introduced plant populations (Bossdorf et al. 2005,
556 Colautti et al. 2009, Felker-Quinn et al. 2013, Colautti & Lau 2015). Thus, rapid phenotypic
557 evolution appears to be common in introduced plant populations after introductions of plant
558 species into a new range.

559 Given the importance of herbivores and pathogens for plant evolution (Strauss &
560 Zangerl 2002) and the often observed release from specialist enemies (Mitchell & Power
561 2003, Meijer et al. 2016), shifts in allocation of resources from specialist to generalist enemy
562 defenses have been predicted in alien plants (shifting-defense hypothesis; Müller-Schärer et
563 al. 2004). Feeding experiments and chemical analyses of common-garden plants confirmed
564 that there are often differences in plant defenses between native and introduced populations,
565 and that defenses is-are reduced against specialists but not generalists (Doorduyn & Vrieling
566 2011, Felker-Quinn et al. 2013). Full support for the shifting-defense hypothesis has been
567 found in *Senecio jacobaea* where resistance to specialists is decreased but levels of
568 pyrrolizidine alkaloids and defense against generalists are increased in introduced populations

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

Commented [WD2]: Do we want to use 'introduced' or 'alien' throughout?

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

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

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

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

612

613 **5.2. Evolutionary Impacts on Native Species**

614 Alien plants can also cause evolutionary responses in native residents. In particular, invasive
615 species are expected to exert selection on native species and cause evolutionary changes in
616 invaded communities (Strauss et al. 2006). While evolutionary studies on alien plants initially
617 focused entirely on alien evolution, recently attention has shifted toward evolutionary
618 responses of native species. For instance, native plants growing together with spotted

619 knapweed (*Centaurea maculosa*) in North America have evolved greater resistance to
620 knapweed allelopathy (Callaway et al. 2005). A combination of selection analyses and
621 reciprocal transplants in California showed that the exotic legume *Medicago polymorpha*
622 alters selection and adaptation of the native *Lotus wrangelianus* (Lau 2006, 2008). Perhaps
623 the most intriguing example of rapid evolution of a native species in response to an invasive
624 plant is the coevolutionary dynamic between invasive *Alliaria petiolata* and native
625 competitors in North America. It was shown that the [level of the](#) glucosinolate sinigrin
626 rapidly evolves in invasive *Alliaria* populations in response to native competitors, but the
627 native *Pilea pumila* equally rapidly evolves greater resistance to ~~these~~ [this](#) allelochemicals
628 (Lankau 2012). This could explain why glucosinolate concentrations decline with population
629 age in *Alliaria* populations in North America (Lankau et al. 2009). Rapid evolution [in](#)
630 [response](#) to invasive plants is common in native plants, as shown by a recent meta-analysis
631 (Oduor 2013). Broadening evolutionary studies of alien plants to their native competitors and
632 antagonists, and the coevolution between aliens and natives, is a promising and important
633 area for future research [\(Figure 1\)](#).

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635 5.3. Molecular Genetics of Invasions

636 In addition to traits, the [ecology and](#) evolution of alien plants has also been studied through
637 molecular genetic analyses. Initially, these were mainly used for identifying pathways and
638 numbers of introductions, and genetic bottlenecks (reviewed in Bossdorf et al. 2005,
639 Dlugosch & Parker 2008). General insights from these studies are (1) contrary to
640 expectations, genetic diversity is often only moderately reduced in introduced populations,
641 (2) multiple introductions are common, and (3) admixture between different introductions can
642 even increase genetic diversity [in the introduced range](#). Since these earlier studies were

643 usually done with neutral markers, they were often disconnected from trait-based studies.
644 More recently, however, researchers have combined molecular with trait data, yielding more
645 powerful evolutionary studies.

646 Molecular data can provide knowledge of introduction pathways, allowing ~~better~~
647 ~~matching of alien populations with native ones for comparison to choose selection of the most~~
648 ~~likely native source populations as comparators for the invasive populations~~ (e.g., Liao et al.
649 2014). One can also incorporate population structure and stochastic processes into trait
650 analyses (Keller & Taylor 2008), analyse trait evolution along an invasion chronosequence
651 (Barker et al. 2017), test for phenotypic consequences of population admixture (Keller &
652 Taylor 2010), or compare specific hybrids or cytotypes of alien species (Hovick & Whitney
653 2014, Parepa et al. 2014).

654 Combining molecular and trait data can also ~~uncover~~ ~~help to answer questions about~~
655 the genetic basis of evolving traits, i.e., the genes or genomic regions associated with
656 phenotypic changes in alien plants (**Figure 1**). Recent advances in sequencing technologies
657 allow high-resolution genomic data generation for any alien plant species, which can then be
658 used to construct genetic maps for Quantitative Trait Loci (QTL) or genome-wide association
659 studies. For example, Whitney et al. (2015) used a single-nucleotide-polymorphism map to
660 identify QTLs underlying fitness variation in invasive sunflowers. Gould & Stinchcombe
661 (2017) used whole-genome sequencing to show that flowering-time variation is associated
662 with different genes in the introduced versus native range of *Arabidopsis thaliana*. The use of
663 high-resolution genomic methods in invasion biology should be increased from now on.

664

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665 **5.4. The Way Forward for Research on the Evolution and Genetics of Invasive Plants**

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

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

690

691 6. CONCLUSIONS

692 In a time of rapid environmental and biotic change, understanding why certain alien species
693 can successfully naturalize and become invasive has become a major objective in ecology
694 and evolution. At the same time, because alien organisms experience novel ecological
695 contexts, they provide study systems that advance our ecological and evolutionary
696 understanding. The ecology and evolution of alien plants is a very broad field crossing
697 different spatial and temporal scales, and with a plethora of hypotheses. We have highlighted
698 some of the major conceptual and methodological advances, as well as empirical results, that
699 we argue moved the field forward in the last decades or will do so in the near future.

700 Although we did not discuss modelling approaches, there have also been major advances in
701 developing more mechanistic models that bear great promise in predicting invasion risks
702 (e.g., Carboni et al. 2018). We call for more transparency on which ‘invasive’ definition
703 people use, and for a dissection of the different dimensions of invasiveness **(Figure 2)**. Using
704 the right comparators and accounting for introduction history may result in more consistent
705 findings. By integrating modern theories on plant coexistence and applying phylogenetic and
706 functional-trait approaches, ~~by integrating mechanistic processes into modelling approaches,~~
707 by studying the interplay between different biotic interactions, and by combining molecular
708 with experimental evolutionary approaches, we will advance our understanding of alien
709 plants and improve predictions on which aliens might invade in the future.

710

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711 **DISCLOSURE STATEMENT**

712 The authors are not aware of any affiliations, memberships, funding, or financial holdings
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714

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719

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1080 **Figure caption**

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1082 **Figure 1**

1083 Visual summary of research intensity, consistency of results and open questions in the study of alien
1084 plant ecology and evolution, including general patterns and drivers, biotic interactions, and the role of
1085 evolution and genetics. We use a four-level heat-colour scale for the different cells to indicate whether
1086 in our opinion, research intensity, consistency of results and open questions have low, moderate, high
1087 or very high values. With arrows, we indicate the trends (decreasing, continuing, increasing, rapidly
1088 increasing) in the rate of research on each topic. For each topic, we list our top question that needs to
1089 be answered to better understand the ecology and evolution of alien plants.

1090

1091 **Figure 2**

1092 The stages and barriers (red bars) of the invasion process (after Richardson et al. 2000) and the
1093 multiple dimensions of invasiveness (e.g. Catford et al. 2016). When a species has been introduced
1094 from its native range across a biogeographic barrier it is an alien. Those aliens that passed the
1095 environmental barrier and are sometimes found in the wild but do not persist are casuals. ~~The~~
1096 ~~ones~~ Those that passed the environmental and reproductive barriers and thus form persistent
1097 populations are naturalized species. A subset of the naturalized aliens is considered invasive.
1098 Invasiveness, however, is not a binary variable but a continuous one and has multiple dimensions (i.e.,
1099 distributional characteristics) indicated by the axes of the cube. Each of these invasiveness dimensions
1100 is associated with some main barrier along the continuum. Invasive species can theoretically occur
1101 anywhere within this multidimensional space. For example, species A is an invasive species that is a
1102 habitat specialist with a small range size that can become locally very abundant, due to overcoming
1103 competition from natives. Species B is an invasive species that has a large range through overcoming
1104 dispersal barriers, but is also a habitat specialist but has a large range and with a low local abundance.

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1105 Species C in an invasive species that has high values for each of the three invasiveness dimensions
1106 shown, and so has overcome competition, dispersal and environmental barriers.;