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1 Title: Disentangling the four demographic dimensions of species invasiveness

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19 impact; invasion ecology; functional traits; four demographic dimensions of
20 invasiveness; non-native plants; Rabinowitz; review & synthesis

21 Type of article: Essay review

22 **Summary**

- 23 1. A definitive list of invasive species traits remains elusive, perhaps due to
24 inconsistent ways of identifying invasive species. Invasive species are typically
25 identified using one or more of four demographic criteria (local abundance,
26 geographic range, environmental range, spread rate), referred to here as the
27 demographic dimensions of invasiveness.
 - 28 2. In 112 studies comparing invasive and non-invasive plant traits, all 15
29 combinations of the four demographic dimensions were used to identify invasive
30 species. 22% of studies identified invasive species solely by high abundance
31 while 25% ignored abundance.
 - 32 3. We used demographic data of 340 alien herbs classified as invasive or non-
33 invasive in Victoria, Australia to test whether the demographic dimensions are
34 independent and which dimensions influence invasive species listing in practice.
 - 35 4. Species' abundances, spread rates and range sizes were independent. Relative
36 abundance best explained the invasiveness classification. However, invasive and
37 non-invasive species each spanned the full range of each demographic dimension,
38 indicating that no dimension clearly separates invasive from non-invasive
39 species.
 - 40 5. Graminoids with longer minimum residence times were more frequently
41 classified as invasive, as were forbs occurring near edges of native vegetation
42 fragments.
- 43 *Synthesis.* Conflating multiple forms of invasiveness by not distinguishing
44 invasive species that are identified using different demographic criteria may
45 obscure traits possessed by particular subsets of invasive species. Traits
46 promoting high abundance likely differ from those enabling fast spread and broad

47 ranges. Examining traits linked with the four demographic dimensions of
48 invasiveness will highlight species at risk of becoming dominant, spreading
49 quickly or occupying large ranges.

50

51 **Introduction**

52 Considerable effort has gone into identifying characteristics associated with species
53 invasiveness (van Kleunen, Weber & Fischer 2010). Knowing that plant species with
54 particular traits, such as short generation times and bird-dispersed seeds, are more
55 likely to become invasive is valuable for biosecurity and weed risk assessment
56 (Weber *et al.* 2009). Notwithstanding some success (Dawson, Burslem & Hulme
57 2009; van Kleunen, Weber & Fischer 2010; Gallagher, Randall & Leishman 2015), a
58 definitive set of traits that reliably predicts invasiveness remains elusive (Pyšek &
59 Richardson 2007; Ordonez, Wright & Olf 2010) and a reliable, rigorous and
60 universal approach for identifying invasive species is lacking (Higgins & Richardson
61 2014). In this essay, we contend that imprecise definitions of invasiveness, and
62 comparing invasive species that are identified based on different demographic criteria,
63 may have obscured links between plant traits and invasiveness.

64 Traits associated with invasiveness are typically identified by comparing the trait
65 values of alien species classified as invasive with those of alien or native species
66 classified as non-invasive (van Kleunen *et al.* 2010). Species are likely to be invasive
67 for different reasons (Rejmánek 2011) and to varying extents, and different definitions
68 of invasiveness are used (Colautti & MacIsaac 2004; Barney *et al.* 2013). Some of the
69 consequences of imprecise and inconsistent invasion definitions have been discussed
70 previously (e.g. confusion of concepts, hindrance to theory, synthesis and

71 communication, Colautti & MacIsaac 2004), but implications of this imprecision for
72 trait-based studies have been largely overlooked.

73 Here we consider how local abundance, geographic range, environmental range and
74 spread rate are used, separately or in combination, to identify invasive species. We
75 call these the four demographic dimensions of invasiveness. Building on
76 Rabinowitz's (1981) seven forms of species rarity, we show that all 15 combinations
77 of the four dimensions ($2^4 - 1 = 15$) are used to identify invasive species in 112
78 studies that contrast the traits of invasive and non-invasive plants (van Kleunen,
79 Weber & Fischer 2010).

80 In order to determine whether the demographic dimensions are correlated, making
81 some redundant in practice, we analysed correlations among the relative abundances,
82 environmental and geographic range sizes, and spread rates of 340 "invasive" and
83 "non-invasive" alien (non-native, introduced) herbs in Victoria, Australia. Accounting
84 for minimum residence time and habitat fragmentation, we find that the dimensions of
85 invasiveness in this dataset are largely independent and that local abundance was the
86 demographic dimension most strongly linked with this invasive species classification.
87 Having demonstrated that species identified as invasive show many different
88 demographic patterns and that no one demographic dimension clearly separates
89 invasive from non-invasive species, we briefly present a few examples of plant traits
90 that might relate to the demographic dimensions. We conclude by outlining a method
91 to strengthen the understanding of traits that promote invasiveness. We focus on
92 plants in this manuscript, but note that similar arguments may apply to other taxa.

93 **Criteria that underpin definitions of invasiveness**

94 Like many terms in ecology (including invasion impacts, Jeschke *et al.* 2014), the
95 definition of “invasive” is disputed (Colautti & MacIsaac 2004). We examined 43
96 definitions of invasiveness provided in 14 key academic reviews, seven
97 environmental policy documents and three invasive species databases to identify
98 criteria typically used to distinguish invasive and non-invasive species (see Table S1
99 in Supplementary Information). These references were selected because they are
100 prominent, highly cited or recent publications that provide specific definitions of
101 invasive species.

102 Criteria typically used to distinguish invasive species from their non-invasive
103 counterparts include species’ local abundance, environmental range size, geographic
104 range size, and rate of spread (Table S1). Direct assessment of negative effect, or
105 impact, is also used (Table S1). These five criteria indicate the fundamental
106 dimensions, or axes, underlying the concept of invasiveness. Not all dimensions are
107 used in all definitions of invasiveness; different combinations of these dimensions are
108 used as criteria for distinguishing invasive and non-invasive species (Table S1). In
109 this paper, we focus on the first four dimensions, which relate to invasive species
110 demography (i.e. abundance and distribution) post-introduction (Table 1). Various
111 measures and indicators can be used to represent the four demographic dimensions
112 (Table 1). For reasons outlined below, we do not explicitly discuss impact in this
113 paper.

114 Either implicit or explicit to the 43 definitions was the need for invasive species to
115 form self-sustaining populations beyond their natural range, which was usually
116 achieved via human introduction (Table S1). We did not include “the ability to form
117 self-sustaining populations” as a criterion of invasiveness because it does not

118 distinguish invasive alien species from alien species that are naturalised but non-
119 invasive. We regard invasiveness as an attribute, or characteristic, of a species.
120 Invasiveness is distinct from invasion success (Catford *et al.* 2012b), which is affected
121 by the abiotic characteristics of the invaded ecosystem, biotic interactions between the
122 invading and resident species, and propagule pressure of the invader (Catford, Jansson
123 & Nilsson 2009).

124 ***Reasons for focusing on the four demographic dimensions of invasiveness***

125 We note that impact is often used as a criterion to identify invasive species and thus
126 acts as a fifth dimension of invasiveness. However, we restrict our focus to the four
127 demographic dimensions in this paper. Our goal is to provide a framework for finding
128 traits that reliably and consistently predict invasiveness. Invasive species impacts
129 include a diverse range of negative ecological, economic, human health and aesthetic
130 impacts (Table S1), so impact itself could be characterised as multidimensional, with
131 relevant traits depending on the impact of concern. Identifying a common suite of
132 impact-related traits is therefore far less likely than identifying a suite of traits related
133 to the other four dimensions of invasiveness, which are more limited in scope.
134 Species' overall impacts are partly determined by their abundance and distributions
135 such that the four demographic dimensions may suffice as indicators of impact.
136 Although species could potentially cause significant harm (and be considered
137 invasive) even if they have low abundance and small ranges, species are most likely
138 to be harmful when their abundances are high and range sizes large (Buckley &
139 Catford 2016). This is illustrated by Parker *et al.*'s (1999) model of invasive species
140 impacts where net impact is a function of species' per capita effects, abundance and
141 geographic range size. Our focus on demography is consistent with some other studies

142 that focus on the ecological aspects of invasiveness (e.g. Ricciardi & Cohen 2007;
143 Wilson *et al.* 2009) (but see Vilà *et al.* 2011; Pyšek *et al.* 2012).

144 **Forms of invasiveness**

145 With the exception of spread rate, the demographic dimensions used to define
146 invasiveness are the same dimensions used by Rabinowitz (1981) when defining
147 species rarity. In her seminal work, Rabinowitz (1981) proposed seven forms of rarity
148 based on combinations of species' local population size (local abundance), geographic
149 distribution (geographic range size) and habitat specificity (environmental range size).

150 Though some combinations may give rise to rare species more often than others
151 (Rabinowitz 1981), she convincingly argues (and subsequently demonstrates,
152 Rabinowitz, Cairns & Dillon 1986) that species can be rare in different ways.

153 The same characteristics that are used to define rarity can be used to define its inverse,
154 commonness, because these characteristics relate to species' abundances and
155 distributions in the landscape (e.g. low abundance can indicate rarity, high abundance
156 can indicate commonness; Table 2). Most invasive species eventually become
157 common (Firn *et al.* 2011; Dawson, Fischer & van Kleunen 2012). It is thus logical
158 that rare and invasive species can be defined using similar criteria (e.g. Carboni *et al.*
159 2016) and, like species that are rare, species that are invasive can be invasive in
160 different ways.

161 Incorporating spread rates into Rabinowitz's scheme gives rise to 15 demographic
162 forms of invasiveness ($2^4-1 = 15$, Table 2; including impact as the fifth dimension
163 would result in $2^5-1 = 31$ forms of invasiveness). Although the demographic forms
164 and demographic dimensions of invasiveness are related, the former result from
165 different combinations of the latter (following Rabinowitz 1981), so they are distinct

166 concepts (Table 2); we refer to both concepts throughout the paper. The most extreme
167 demographic form of invasiveness would comprise invasive species that reach high
168 local abundance and have broad geographic ranges, wide environmental ranges and
169 fast spread rates (AEGS in Table 2). Although presented as distinct forms of
170 invasiveness, it is important to note that the dimensions underlying these 15 forms are
171 continuous and are not demarcated by thresholds that distinguish e.g. high abundance
172 from low abundance. Thresholds may be found that enable categorisation, but it will
173 likely be more informative to retain continuous dimensions in any trait-based analyses
174 (see Discussion; Carboni *et al.* 2016).

175 We reviewed a sample of the trait-based invasion literature to determine whether all
176 15 forms of invasiveness are used to identify invasive species and whether a particular
177 form may be used more than others. Our sample consisted of 112 field or
178 experimental-garden studies that compared the trait values of invasive alien species
179 with non-invasive species, as used by van Kleunen *et al.* (2010) in their meta-analysis
180 examining invasive species traits [we were unable to access 6 of the 118 papers used
181 by van Kleunen *et al.* (2010)]. We chose this sample of papers because each of the
182 studies specifically contrasted invasive and non-invasive species in an attempt to
183 identify the traits that distinguish them and, as such, presumably had strong reasons
184 for distinguishing the two types of species. Specific definitions of invasiveness were
185 rarely presented in the 112 studies, but most authors stated their rationale for species
186 selection; we used this information to represent the criteria used to distinguish
187 invasive and non-invasive species (Table S2). Critically, even if a species was
188 classified as being invasive based solely on its abundance, this does not necessarily
189 mean that the species had slow spread rates or small ranges. Rather, it indicates that
190 the other three demographic dimensions were not used as criteria of invasiveness

191 (Table 2, Figure 1), so the species could be distributed anywhere along those
192 dimensions (e.g. high, low or medium spread rates).

193 The 112 studies used all 15 demographic forms of invasiveness (Fig. 1, Table 2): all
194 four demographic dimensions were used and some definitions shared no common
195 criteria. If impact was included as the fifth dimension, 28 of 31 forms were used, but
196 impact was never used as a criterion by itself (Table S2; 62% of the 112 studies did
197 not use impact to identify invasive species, indicating that species can be considered
198 invasive without necessarily having negative impacts). Of the four demographic
199 dimensions, abundance was most commonly used (66% of studies) and 22% of
200 studies identified invasive species solely on abundance. However, 25% of the 112
201 studies did not include abundance as a criterion (Fig. 1), meaning that the invasive
202 species featured in these 28 studies could potentially occur at low abundances, in
203 contrast to the species in 74 studies that must reach high local abundance. After
204 abundance, geographic range size was the next most commonly used demographic
205 criterion (44%), followed by spread rate (38%). Environmental range was the least
206 used criterion (22% of studies). Eight studies did not document the rationale for
207 species selection, and two studies referred to databases for lists of invasive species. A
208 single criterion was used to identify invasive species more frequently than multiple
209 criteria (36% of studies used one criterion), but 34% of studies relied on two criteria
210 (19% used three criteria; 3% used four criteria; 9% used none of the four demographic
211 criteria).

212 **Are the demographic dimensions of invasiveness independent in practice?**

213 Our review of 112 studies illustrates that invasive species are identified in many ways
214 using multiple criteria, indicating support for multiple dimensions of invasiveness.

215 However, a single dimension may be used in practice, or the four demographic
216 dimensions may be highly correlated such that abundant alien species are also those
217 with fast spread rates, wide geographic ranges and broad environmental ranges. We
218 assessed whether each of the four demographic dimensions of invasiveness was
219 correlated with an invasive species classification using a case study of alien plant
220 species in Victoria, a 237,629 km² state in south-eastern Australia.

221 We used an existing classification scheme to identify species that are considered
222 invasive and non-invasive (Carr, Yugovic & Robinson 1992). Based on observations
223 made over 25 years in public and private land, together with published and
224 unpublished information, the three experts (Carr, Yugovic and Robinson) generated
225 the classification based on the perceived threat that alien species pose to “one or more
226 native vegetation formations” (examples of the 15 broad vegetation formations:
227 riparian vegetation, dry coastal vegetation, cool temperature rainforest) (Carr,
228 Yugovic & Robinson 1992). This is the only invasive species classification specific to
229 the whole state of Victoria that is based on the threat that alien species pose to natural
230 ecosystems (other state-wide Victorian schemes relate to weeds of agricultural
231 systems). The authors did not specify the exact criteria used in their assessments, but
232 given the influence of species’ demography on species’ overall impacts, we reasoned
233 that the demographic dimensions would likely have informed the classification [this
234 was subsequently confirmed by Geoff Carr, the lead author of the classification].

235 Use of the existing Carr *et al.* classification allowed us to: 1) assess the independence
236 of the demographic dimensions of invasiveness for a large suite of plant species and
237 the likely existence of different forms of invasiveness; and 2) determine whether
238 species’ demography (as represented by the demographic dimensions of invasiveness)

239 relates to species' (perceived) ecological impacts (as represented by the Carr *et al.*
240 classification), as theory would predict (Buckley & Catford 2016). Being based on the
241 overall threat that alien species pose to native vegetation, which likely takes into
242 account species' per capita effects plus demography, the Carr *et al.* scheme enabled us
243 to avoid circularity that would stem from testing, for example, an abundance-based
244 classification scheme using data on species' abundances.

245 We used plant occurrence and cover data for 2714 taxa that are alien (non-indigenous)
246 to Victoria (149,772 presence records from 1900 through 1991 from Victoria's Flora
247 Information System (FIS) and Australia's Virtual Herbarium; 19,057 abundance
248 records from 1970 through 1991 from FIS, which were collected from areas not
249 directly modified by intensive human land use; Appendix S1). Observations before
250 1900 were imprecise. We set the end date as 1991 so that the modeled data
251 corresponded with information that would have informed the 1992 invasive species
252 classification (Carr, Yugovic & Robinson 1992). We limited analyses to alien species
253 that had at least 20 presence records and the necessary demographic data (391
254 species). Of these 391 species, Carr, Yugovic and Robinson (1992, p.15) had
255 classified 259 of them as either: "not a threat (but may have a negative visual
256 impact)" (14 species); "potentially serious threat to one or more vegetation
257 formations" (72 species); "serious threat to one or more vegetation formations" (99
258 species); or "very serious threat to one or more vegetation formations" (74 species).
259 The demographic characteristics (described below) of potentially serious, serious and
260 very serious threat species were indistinguishable from each other, so we combined
261 these three types of species into one category, which we call "invasive" (245 species).
262 We assigned 132 unclassified alien species to the "not a threat" category, which we
263 call "non-invasive" (146 species). Carr, Yugovic and Robinson (1992) considered all

264 alien species naturalized in Victoria in their assessment, but restricted their
265 classification to a subset of alien plants considered environmental weeds, which
266 “invade native vegetation, usually adversely affecting survival of the indigenous
267 flora” (p. 4). This indicates that unclassified taxa were not considered a threat to
268 native vegetation and only differ from the 14 classified “no threat” species in that the
269 latter may have a visual (but not ecological) impact; we are not concerned with
270 aesthetics here.

271 Species’ *local abundance* was represented by the maximum cover abundance of each
272 taxon calculated as a proportion of summed species cover in 30 m × 30 m survey
273 plots. We use proportional cover, rather than absolute cover, because it accounts for
274 variation in site productivity and the abundance of other species (Catford *et al.*
275 2012b), and accords with the way abundance is usually related to invasiveness in the
276 literature (Table S2).

277 Species’ *environmental range sizes* were represented by the geometric mean of the
278 standard deviations of four uncorrelated ($|r| < 0.6$) environmental variables at
279 locations where species were detected [maximum temperature in warmest quarter
280 (°C), precipitation in coldest quarter (mm), soil radiometric thorium concentration
281 (radioelement count; indicates soil texture and fertility, Pracilio *et al.* 2006) and
282 topographic wetness index, Appendix S1] following Catford *et al.* (2011). The four
283 variables can be incorporated into one metric because the scales on which original
284 data are measured do not influence relative changes in geometric means (McCarthy *et*
285 *al.* 2014). We use standard deviations rather than ranges (i.e. maximum minus
286 minimum) to account for potential differences in sampling effort (Burgman 1989).

287 We estimated species' geographic ranges using the latitude and longitude of locations
288 in which species were recorded. *Geographic range size* was represented by the
289 geometric mean of the standard deviations of latitude and longitude.

290 Species' *rate of spread* was estimated by fitting self-starting logistic models (*nls*
291 function in R) to occurrence data, which indicated the time elapsed between
292 successive observations, and the cumulative distance of these observations from the
293 point of origin (location of earliest recorded presence in Victoria). The predicted
294 distance, D_{it} , spread by taxon i after time t has elapsed is given by:

$$295 \quad D_{it} = asym_i / (1 + \exp((mid_i - t) / scal_i))$$

296 where $asym_i$ is the asymptotic spread distance for taxon i , mid_i is the time at which
297 taxon i has spread to half its asymptotic spread, and $scal_i$ is the time elapsed between
298 reaching half and $1/(1 + e^{-1})$ (approximately three quarters) of its asymptotic spread.
299 For each taxon, maximum spread rate was approximated as the gradient between the
300 points on the curve at $t = mid_i$ and $t = mid_i + scal_i$.

301 In their assessments of alien species threat, Carr, Yugovic and Robinson (1992) may
302 have accounted for the time available for populations of each species to grow and
303 spread, or the strength of species' associations with anthropogenic habitats (e.g. they
304 may have down-weighted the risk of species that only occur at the edges of vegetation
305 fragments and around human settlements). We therefore quantified minimum
306 residence time (MRT) to account for time since introduction and distance to edge
307 (akin to habitat fragmentation) to jointly account for variation in propagule pressure
308 and human disturbance (Catford *et al.* 2011), which may facilitate invasion (Pyšek *et*
309 *al.* 2015). MRT was calculated as the number of years between the first recorded
310 observation (from 1900 onwards) in native-dominated vegetation in Victoria and

311 1992. For each species, we quantified the mean distance between each observation
312 and the edge of the associated vegetation fragment (e.g. distance to road, distance to
313 crops).

314 We analyzed correlations among local abundance, environmental and geographic
315 range sizes, spread rate, MRT and mean distance to edge. We used logistic regression
316 to estimate relationships between the probability of taxa being classified as invasive,
317 and the four demographic dimensions of invasiveness, MRT and mean distance to
318 edge (cover abundance and distance to edge were log-transformed).

319 The probability that taxon i was classified as invasive was:

$$320 \text{logit}(p_i) = t_{f[i]} + u_{f[i]}a_i + v_{f[i]}e_i + w_{f[i]}g_i + x_{f[i]}s_i + y_{f[i]}m_i + z_{f[i]}d_i$$

321 where $t_{f[i]}$ is the intercept term for taxon i of growth form f , the values of u , v , w , x , y
322 and z are the other regression coefficients that are estimated, and a_i , e_i , g_i , s_i , m_i and d_i
323 are the local abundance, environmental range, geographic range, spread rate, MRT
324 and mean distance to edge, respectively, for taxon i . All analyses were performed with
325 R 3.1.1 (R Core Team 2014).

326 We only present results from the models based on forbs (240 species: 132 invasive,
327 108 non-invasive) and graminoids (100 species: 69 invasive, 31 non-invasive),
328 because few records were available for woody species (44 species) and other growth
329 forms (7 species).

330 ***Results and discussion of the Victorian analysis***

331 Apart from a positive correlation between the sizes of species' environmental and
332 geographic ranges, which was expected, the demographic characteristics of alien

333 herbs in Victoria were not strongly correlated (Fig. 2; MRT and distance to edge were
334 also independent, with all correlations $|r| < 0.5$, Table S3). This illustrates that species
335 in the dataset that reach high relative abundance, for example, are no more or less
336 likely to have fast spread rates or broad geographic and environmental ranges than
337 species with low relative abundance.

338 The demographic characteristics of invasive and non-invasive species varied, with
339 invasive and non-invasive species spanning each demographic dimension of
340 invasiveness (Fig. 2). This means that species with high and low abundances, fast and
341 slow spread rates, and wide and narrow ranges were all defined as invasive, indicating
342 that some demographic characteristics of some invasive species contradict the
343 demographic characteristics of other invasive species. Despite this variation, the
344 probability of graminoids and forbs being classified as invasive, rather than non-
345 invasive, increased with abundance (Figs 3 & 4, Table S4). The only other significant
346 relationship between the invasive species classification and the demographic
347 dimensions was geographic range for graminoids.

348 Contrary to expectations, the probability of a graminoid being classified as invasive
349 (as opposed to non-invasive) decreased with increasing geographic range sizes. This
350 may reflect an assessment by Carr, Yugovic and Robinson (1992) that graminoids
351 with wide distributions posed less of a threat to native vegetation than graminoids
352 with narrow distributions because the former had already filled most of their potential
353 range and exerted their impacts. The negative relationship could also reflect our
354 methodological approach, which restricted analyses to species with ≥ 20 observations.
355 This threshold was essential for calculating representative range sizes, but also meant
356 that non-invasive species, which are perhaps more likely to have small ranges than

357 invasive species, were disproportionately excluded (78% of the graminoids and forbs
358 with <20 presence records were classified as non-invasive, whereas 41% of the
359 species with ≥ 20 presences were classified as non-invasive).

360 Graminoids with longer minimum residence times were more likely to be classified as
361 invasive than graminoids with shorter MRT (Fig. 4). There were no correlations
362 between species demography and MRT, suggesting that, for graminoids, species
363 introduced earlier may have been more likely to exert impacts (not assessed here).
364 Alternatively, Carr *et al.* may have been more familiar with graminoids introduced
365 earlier than graminoids introduced later. Forbs classified as invasive were generally
366 recorded closer to the edge of vegetation fragments than forbs classified as non-
367 invasive. This was surprising, as alien species that invade intact native vegetation
368 would presumably pose a greater threat to native plant species – the aim of Carr *et*
369 *al.*'s classification. The greater visibility (and therefore familiarity to Carr *et al.*) of
370 alien forbs at the edge of vegetation fragments (compared to alien forbs in the interior
371 of fragments) may have affected the classification of these species.

372 Species' maximum relative cover appears to be a key characteristic underlying Carr *et*
373 *al.*'s (1992) risk ratings, so traits related to abundance may help predict this particular
374 classification. However, not every species with high abundance was listed as invasive
375 and *vice versa*. For example, *Urtica urens* L. had the 24th highest proportional cover
376 (32%) among 240 forbs but was classified as no threat by Carr *et al.*, yet *Emex*
377 *australis* Steinh., with a maximum observed cover of 2%, was classified as invasive.

378 Although we found that species abundance was correlated with Carr *et al.*'s threat-
379 based classification, we also highlight that some species can be listed as invasive for
380 reasons that are unrelated to their observed demography. *Eragrostis curvula* (Schrad.)

381 Nees is classified as invasive in Victoria despite being ranked 99th for relative
382 abundance, 86th for environmental range, 67th for geographic range and 81st for spread
383 rate out of 100 invasive and non-invasive graminoids. Its classification may reflect
384 high per capita effects, which may result in this species reaching a high threat status
385 despite its seemingly benign demography. The classification of *E. curvula* as invasive
386 may also reflect evidence of its invasiveness elsewhere, or that the abundance data
387 were collected from plots used to characterize native vegetation and thus are not a
388 random sample of Victoria's vegetation.

389 The Victorian analysis illustrates that species are classified as invasive for different
390 reasons and invasive species can exhibit several distinct demographic characteristics.
391 Apart from geographic and environmental range size, the dimensions were
392 independent of each other, indicating that three of the four demographic dimensions
393 inform this invasive species listing and that multiple forms of invasiveness exist in
394 Victoria. Local abundance was the main predictor of the classification, but some forbs
395 and graminoids were classified as invasive for reasons other than their abundance. If
396 searching for traits related to invasive forbs and graminoids in Victoria, it would
397 therefore be worthwhile distinguishing among these different forms of invasiveness
398 by examining traits related to three of the demographic dimensions (because of their
399 strong correlation, it would only be necessary to examine traits related to geographic
400 range size *or* environmental range size, not both).

401 Although local abundance was the main predictor for this threat-based invasive
402 species list, the key demographic dimension may vary for other groups of taxa, in
403 other places and for invasive species lists compiled by other people.

404 **Discussion**

405 Our examinations of key definitions of invasiveness (Table S1), criteria used to
406 identify invasive species (Fig. 1, Table S2), and the demographic characteristics of
407 alien species in Victoria (Figs 2-4) together provide strong evidence that invasiveness
408 is multidimensional and many forms of invasiveness exist. The variety of ways
409 invasive species are defined and identified reflects the biological reality that species
410 become invasive in different ways. Even though some definitions share no common
411 criteria, most classifications and studies of species invasiveness categorise species as
412 either invasive or not (though some specify different strengths of invasiveness, e.g.
413 major, minor or non-weeds, Speek *et al.* 2013). This implies that multiple – possibly
414 contradictory – forms of invasiveness are routinely condensed into a single form.
415 Conflating different forms of invasiveness is problematic in that it could obscure traits
416 linked with invasiveness, as species that spread rapidly may possess different traits to
417 those that reach high local abundance. To paraphrase Rabinowitz (1981), failure to
418 discriminate among the forms of invasiveness represents a lost opportunity to
419 investigate the causes and consequences of their differences.

420 ***Demographic dimensions of invasiveness may be associated with different***
421 ***functional traits***

422 Based on current ecological understanding, it seems likely that the functional traits
423 related to the four demographic dimensions differ. We briefly note a few examples.
424 By helping populations grow from a small size, self-compatibility (Lovett-Doust
425 1981) and clonality (Rejmánek 2011) should facilitate high local abundance and fast
426 spread rates, but these traits should be less important for range sizes. The ability to
427 disperse long distances should be crucial for achieving fast spread and wide
428 geographic range sizes (Nathan *et al.* 2008), but should not facilitate high local

429 abundance or broad environmental ranges. High phenotypic plasticity, genetic
430 polymorphism and outcrossing can increase intraspecific variation and should
431 therefore facilitate broad environmental ranges (Sultan 2001; Pohlman *et al.* 2005;
432 Rejmánek 2011). These three traits may be indirectly related to geographic range
433 because of correlations between environmental and geographic range sizes, but they
434 are unlikely to correlate with local abundance and spread rate.

435 Some traits may relate to some dimensions and not others, but of greater concern is
436 the potential for contradictory relationships where traits are positively correlated with
437 one dimension and negatively correlated with another. Fast relative growth rates can
438 contribute to high local abundance in disturbed ecosystems, but species with broader
439 environmental ranges typically have slower growth rates than species with narrower
440 environmental ranges (Tilman 1982). In this situation, relative growth rates (and
441 associated traits, e.g. specific leaf area, plant size; Rejmánek 2011) may be positively
442 related to one dimension of invasiveness (local abundance) but negatively to another
443 (environmental range). Habitat generalists could be expected to have broad
444 environmental ranges whereas habitat specialists may be more likely to reach high
445 local abundance. Traits associated with colonisers versus competitors could similarly
446 contribute to different dimensions of invasiveness.

447 ***Potential implications of conflating demographic dimensions***

448 Current understanding suggests that plant traits relate to local abundance, spread rate,
449 and geographic and environmental range sizes in different and sometimes contrasting
450 ways. If studies identify invasive species using different demographic dimensions, it
451 may therefore be hard to ascertain the functional traits associated with invasiveness.
452 Though it would be undesirable if trends were rendered weak, uncertain or

453 inconsistent because of this issue, a greater concern is that traits might be overlooked
454 altogether, despite being strongly related to a dimension of invasiveness. Below, we
455 outline four main ways in which conflating dimensions may obscure trait-based
456 trends.

457 *a) Traits investigated are unrelated to the demographic dimension of invasiveness of*
458 *interest*

459 Traits selected for analysis should be ecologically meaningful and relate to the
460 process of interest (Violle *et al.* 2007). As an example, imagine that a trait like
461 clonality is strongly linked with local abundance, but is unrelated to environmental
462 range. Consider two studies of invasiveness that both measure clonality, but one study
463 uses abundance to identify invasive species and the other study uses environmental
464 range. The expected outcomes are a positive relationship and null relationship
465 respectively. A meta-analysis would conclude weak and uncertain effects of clonality,
466 whereas – in reality – clonality had inconsistent relationships with the underlying
467 dimensions of invasiveness. Without explicitly considering the dimensions of
468 invasiveness being examined, researchers may unwittingly study inappropriate traits
469 because of a desire to assess the generality of a previously observed trend. This may
470 partly explain cases where traits are found to be related to invasiveness in some
471 studies, but not others (e.g. seed mass, Pyšek & Richardson 2007).

472 *b) Traits can relate to multiple demographic dimensions of invasiveness but in*
473 *contrasting ways*

474 Some traits may relate to multiple dimensions of invasiveness because dimensions
475 may share underlying population characteristics (e.g. long-distance dispersal should
476 be positively linked with both spread rate and geographic range size), or because of

477 life history tradeoffs and phylogenetic conservatism (van Kleunen, Weber & Fischer
478 2010). Although traits that have a consistent interpretation across multiple dimensions
479 of invasiveness would make robust indicators, there are many cases where
480 contradictory trait-based trends seem likely (e.g. traits related to colonisation versus
481 competitive ability, and habitat generalists versus habitat specialists, noted above).
482 The way to interpret some traits is even unclear within a single dimension. Having
483 many, light seeds can facilitate high local abundance by increasing the probability of
484 arriving in a safe site suitable for germination, but seedlings from large seeds have a
485 higher probability of establishing in any given site (Muller-Landau 2010). Also within
486 the abundance dimension, traits associated with high abundance in disturbed
487 ecosystems are often in contrast to those associated with high abundance in
488 undisturbed ecosystems (Tilman 1982; van Kleunen, Weber & Fischer 2010). Without
489 knowledge of the local conditions for invasion, it is unclear how to interpret effects of
490 seed mass and “coloniser” traits on species’ local abundance because of tradeoffs
491 between seed size and seed number, and tradeoffs between species’ colonisation and
492 competitive abilities.

493 *c) Invasive and non-invasive species used in comparisons have similar demographic*
494 *characteristics*

495 To find trait-based trends that relate to the demographic dimensions of interest,
496 invasive and non-invasive species must be identified using the same criteria, albeit
497 representing different ends of the spectra. Some native species can have similar
498 demographic characteristics to invasive alien species [both may be spreading
499 (Thompson, Hodgson & Rich 1995), abundant (Firn *et al.* 2011) or common
500 (Dawson, Fischer & van Kleunen 2012)], so invasive alien species should not simply
501 be compared with any native species. Acknowledging this, many comparative studies

502 exclude native species that are known to be invasive elsewhere (van Kleunen, Weber
503 & Fischer 2010). However, rather than relying on criteria reported in invasive species
504 definitions, it would be much more reliable to identify suitable study species using
505 data about their abundance, spread rate and range sizes.

506 Accounting for alien species' residence time and propagule pressure, especially for
507 alien-alien comparisons, is also essential for ensuring that comparisons of species'
508 invasiveness are robust. Some species may have low abundance or a small range not
509 because of their traits, but because they have had insufficient time to grow and spread.

510 *d) Rationale for invasive species listing is inaccurate or imprecise*

511 Invasive species classifications commonly use expert-opinion derived from
512 observation (Burgman 2004; McGeoch *et al.* 2012; Speek *et al.* 2013). Even if precise
513 definitions are provided, people may be unaware of their own underlying motivations
514 for listing some species as invasive because of cognitive biases (Burgman 2001;
515 Hulme 2012). For example, a researcher may believe that they have classified a
516 species as invasive because of its ability to spread rapidly, but this perception may in
517 fact be the result of the species reaching high abundance over a large geographic
518 range. Many authors do not provide specific definitions of invasiveness, instead
519 providing broad definitions that encompass several options (Burgman 2001;
520 McGeoch *et al.* 2012). As a consequence, even species (seemingly) identified using
521 the same criteria may be incomparable. Using empirical data, like in the Victorian
522 analysis above, avoids the potential problems of expert-derived classifications.

523 *A way forward*

524 *a) Focusing on the demographic dimensions of invasiveness*

525 Being more explicit about the demographic dimensions of invasiveness (Colautti &
526 MacIsaac 2004), and the population characteristics and ecological mechanisms
527 underlying these dimensions (Gurevitch *et al.* 2011; Rejmánek 2011), will aid
528 understanding of invasions and will help extrapolate findings gained from a limited
529 suite of invaders to a broader pool (Rejmánek 2011). The value of a more mechanistic
530 approach is illustrated by advances in conservation biology following the
531 differentiation of small versus declining populations (Caughley 1994), gains in
532 understanding of bird extinction risk by relating species ecological characteristics to
533 environmental threats (Owens & Bennett 2000), and by recent work in invasion
534 biology that identifies plant traits related to different stages of invasion (Dawson,
535 Burslem & Hulme 2009; Pyšek *et al.* 2015).

536 *b) The importance of a comprehensive approach*

537 It is important to account for propagule pressure, time since introduction,
538 environmental conditions and characteristics of the recipient community when
539 assessing invasiveness traits as these factors can affect invasion success (Wilson *et al.*
540 2007; Catford, Jansson & Nilsson 2009; van Kleunen, Weber & Fischer 2010;
541 Rejmánek 2011; Gallagher, Randall & Leishman 2015; Pyšek *et al.* 2015). For
542 example, the range sizes and abundance of species will be sensitive to the amount of
543 time that species have had to invade. Despite a growing body of research (Ordonez,
544 Wright & Olf 2010; Tingley *et al.* 2014; Pyšek *et al.* 2015), the combined influence
545 of these factors is rarely examined in trait-based studies of invasiveness. To illustrate,
546 at least 76% of the invasive species included in the 112 studies were associated with
547 humans (1% not associated, 23% association not reported), in contrast to only 8% of
548 the non-invasive species (18% not associated, 74% association not reported), yet only

549 one study explicitly accounted for species' human association in their analyses (i.e.
550 Grotkopp, Erskine-Ogden & Rejmánek 2010, Table S2). A strong association with
551 humans through widespread planting and dispersal, for example, may elevate the
552 propagule pressure of certain species (Catford *et al.* 2012a), disentangling the
553 relationship between their ecophysiological traits and their demography. Completely
554 separating human- and species-mediated propagule pressure is likely to be difficult
555 (Colautti, Grigorovich & MacIsaac 2006), but including a covariate that represents the
556 strength of human association in analytical models should help (Wilson *et al.* 2007).

557 *c) An analytical approach that offers greater nuance*

558 Rather than relying on reported classification criteria and the ability of experts to
559 distinguish invasive from non-invasive species (McGeoch *et al.* 2012), we
560 recommend avoiding invasive species lists altogether when searching for invasiveness
561 traits, instead focusing on demographic data that relate to invasiveness (provided that
562 data are not compromised by weed control). Regressing species' trait values against
563 their abundance, spread rates and the size of their geographic and environmental
564 ranges would help to identify the traits that are most strongly related to the
565 demographic dimensions of invasiveness, and would negate the need to identify a
566 threshold beyond which species are considered invasive (this applies to 15 forms of
567 invasiveness as well). Hierarchical trait-based models seem well suited to such a task
568 (Pollock, Morris & Vesk 2012) and would enable species origin to be included as a
569 covariate. A Bayesian framework would enable information about species'
570 demographic characteristics in other regions to be included as priors.

571 *d) Attributes of good indicators*

572 One of the chief purposes of identifying invasiveness traits is to predict the likelihood
573 of new species becoming invasive. A universal set of traits is unlikely but, like any
574 indicator, traits must possess certain characteristics to be useful indicators (Catford *et*
575 *al.* 2012b). Traits should be ecologically meaningful (i.e. functional, sensu Violle *et*
576 *al.* 2007) by linking the autecology of species to the way in which they are invasive.
577 The traits (and the way the traits are examined, e.g. relative to co-occurring native
578 species; Ordonez, Wright & Olf 2010) must be unambiguous where the meaning and
579 interpretation of a trend is clear. Traits should have consistent effects and be widely
580 applicable and comparable across organisms, ecosystems and regions.

581 **Conclusion**

582 Plant traits that are associated with species invasiveness are used to guide weed risk
583 assessment and management. Rather than searching for traits that distinguish two
584 types of species – invasive or non-invasive, we posit that it will be far more fruitful to
585 look for traits associated with the four demographic dimensions of invasiveness and
586 the multiple forms of invasiveness that they produce. Comparing like with like should
587 lead to more accurate conclusions about the traits commonly possessed by invasive
588 species.

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597 **Data Accessibility**

598 The data used in the Victoria case study is available through the Victorian
599 Biodiversity Atlas (<https://vba.dse.vic.gov.au/vba/index.jsp>) and the Atlas of Living
600 Australia (http://bie.ala.org.au/search?qc=data_hub_uid:dh2 and associated R package
601 ALA4R <https://github.com/AtlasOfLivingAustralia/ALA4R>). All other data is present
602 in the paper and its supporting information.

603 **Supporting Information**

604 Appendix S1: Details of the data, data processing and modeling approach used for the
605 Victoria case study.

606 Table S1: Criteria used to distinguish invasive from non-invasive species from a
607 sample of academic papers (n = 14), policy documents (n= 7) and invasive species
608 databases (n = 3).

609 Table S2: Criteria used to identify invasive species in the 112 studies that compared
610 traits of invasive and non-invasive plant species.

611 Table S3: Pearson correlation coefficients for local abundance, environmental range
612 size, geographic range size and spread rate for alien a) herbs (n = 340), b) forbs (n =
613 240) and c) graminoids (n = 100) in Victoria.

614 Table S4: Results of logistic regressions that model the relationship between the
615 probability of alien herbs being listed as invasive in Victoria and their local
616 abundance, environmental range size, geographic range size, spread rate, minimum

617 residence time and mean distance to edge: a) forbs (n = 240) and b) graminoids (n =
618 100).

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812 **Table 1.** The four demographic dimensions of invasiveness with examples of definitions that use them as criteria (underlined), ways in which
 813 they can be quantified, possible indicators and measures, and some potential management implications of focusing on a given dimension when
 814 designating species as invasive. As well as the indicators and measures listed here, we provide other examples of potential measures in the case
 815 study that compares the demography of invasive and non-invasive species in Victoria.

Dimension	Description	Example of definition	Quantification method	Indicators	Management implications
Local abundance	Refers to species' cover, biomass, density or number of individuals at a site, usually in terms of their relative abundance or dominance.	“Invasive species can quickly transform biological communities due to their <u>high abundance</u> and	Field surveys; remote sensing. The relative contribution that taxa make to different life forms or structural components can help to account for differences in taxon size (Catford <i>et al.</i> 2012b).	Proportion of total vegetation cover or biomass composed of alien species;	Prioritizes management of alien species that dominate standing vegetation, even if only over a small area, allowing management resources to be highly targeted spatially and temporally, e.g. to coincide with stages of population growth that are more sensitive to herbicide (Lindenmayer <i>et al.</i> 2015). If aiming to

		strong impacts on native species” (Lankau <i>et al.</i> 2009, p. 15362).		density.	limit the geographic range of a species, it can sometimes be optimal to control abundant populations that supply most propagules, but at other times it can be optimal to control low-density satellite populations that contribute more to spread (Epanchin-Niell & Hastings 2010).
Geographic range size	Refers to size or spatial extent of species’ distributions.	“Stage V: <u>Widespread</u> and dominant” (Colautti & MacIsaac 2004, p. 138).	Species presence records from e.g. herbaria to characterise latitudinal and longitudinal distributions. Although the (ultimate) area of invasive species occupancy is probably of	Range or standard deviation of latitude and longitude; areal	Focuses management resources on species that occur over vast areas of the landscape, even if at low numbers, presenting challenges for logistics, resourcing and detectability (Hauser & McCarthy 2009). The larger the range size of a species, the more expensive the

			most concern, we suggest using the extent of occupancy as species will likely infill their range with time (see Gaston & Fuller 2009 for potential measures).	extent of occupancy .	cost of control and the lower the likelihood of eradication or containment. As the size of the invaded area increases, there is less uninvaded land to protect from damages, reducing benefits of control (Epanchin-Niell & Hastings 2010).
Environmental range size	Refers to the range of abiotic conditions in which a taxon resides. Proxies include species' latitudinal or altitudinal range	“Invasive (E): Fully invasive species, with individuals dispersing, surviving and reproducing at	Species' environmental range sizes can be characterised through species distribution modelling or by the diversity of habitats that species occupy.	Number of habitat types a species occupies; range of environme	Management would target species that occur across a broad range of environmental conditions and habitat types. The efficacy of invasive species detection and management can vary depending on the environmental conditions of the invaded area, like terrain

	or the number and diversity of habitat and ecosystem types that species occupy. The dimension least referred to in definitions of invasiveness.	multiple sites <u>across a greater or lesser spectrum of habitats</u> and extent of occurrence” (Blackburn et al. 2011, p. 337).		ntal conditions.	and native vegetation structure (Hauser <i>et al.</i> 2016), so different approaches will likely be optimal under different environmental conditions. Invasive species control programs often aim to protect particular ecosystems from invasion impacts (Downey <i>et al.</i> 2009), so targeting species that are listed as invasive solely because of broad environmental ranges seems an unlikely management goal.
Spread rate	Refers to change in spatial extent over time. Most	“Alien species were designated as invasive if	The most challenging demographic metric to quantify, requiring	Distance a species’ range front	Targets rapidly expanding populations. Early detection and intervention presents the best chance of containing species

definitions do not specify actual spread rates, instead describing invasive populations as those that spread or those that spread rapidly.

there was... rapid range expansion or population growth in the introduced country" (McGeoch et al. 2010, p. 1 of Appendix S3).

information about where and when species were introduced and records of how they have moved across the landscape. Many modelling approaches are available (Wilson *et al.* 2007; Andrew & Ustin 2010; Caplat, Nathan & Buckley 2012).

increases over a specific period of time.

before geographic range and number of satellite populations become too large (Hobbs & Humphries 1995). Individuals on edge of population range may be more heavily targeted in control, or populations at the edge of a range (or abutting a potential dispersal barrier) may be supplemented with individuals that have lower dispersal capability, reducing both the rate and probability of continued spread (Phillips *et al.* 2016).

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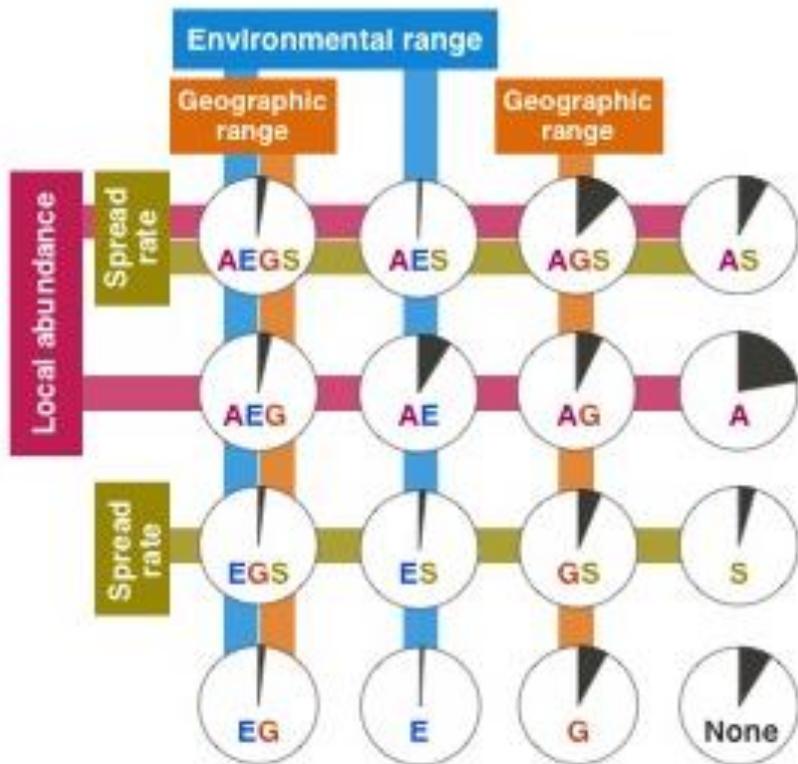
818 **Table 2** A typology of 15 forms of invasiveness based on combinations of the four demographic dimensions: high local abundance (A), broad
 819 environmental range (E), wide geographic range (G) and fast spread rate (S). Adapted from Rabinowitz (1981). Adding the fifth dimension,
 820 impact, would increase the forms of invasiveness to 31 (i.e. each of the 15 forms, with and without impact, plus impact by itself).

Environmental range		Used		Not used	
Geographic range		Used	Not used	Used	Not used
Abundance	Spread rate				
Used	Used	AEGS Fast spreading and locally abundant over a broad range of environmental conditions and a large geographic area.	AES Fast spreading and locally abundant over a broad range of environmental conditions.	AGS Fast spreading and locally abundant over a large geographic area.	AS Fast spreading and locally abundant.
Used	Not used	AEG Locally abundant over a broad range of environmental conditions and a large geographic area.	AE Locally abundant over a broad range of environmental conditions.	AG Locally abundant over a large geographic area.	A Locally abundant.

	Used	EGS Fast spreading over a broad range of environmental conditions and a large geographic area.	ES Fast spreading over a broad range of environmental conditions.	GS Fast spreading over a large geographic area.	S Fast spreading.
Not used	Not used	EG Occurs over a broad range of environmental conditions and a large geographic area.	E Occurs over a broad range of environmental conditions.	G Occurs over a large geographic area.	--

15 forms of invasiveness

Combinations of the demographic dimensions of invasiveness

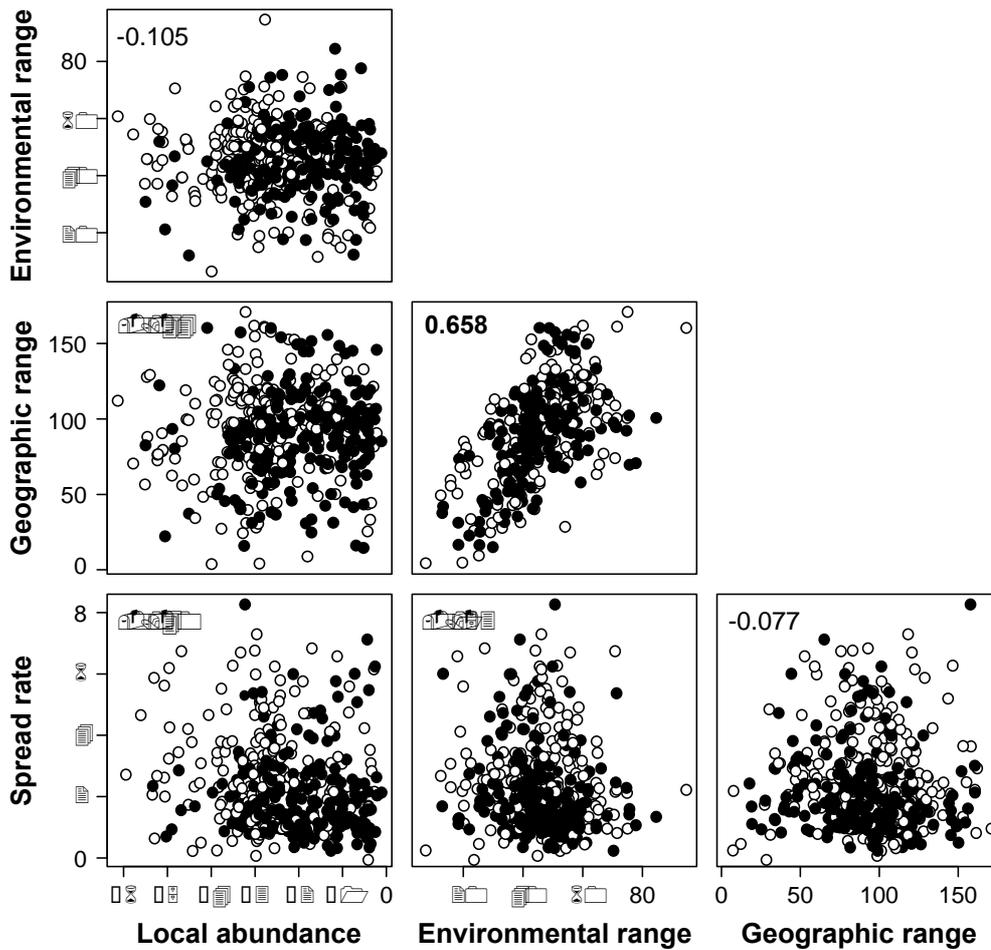


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822 **Fig. 1.** Proportion of 112 trait-based invasion studies that classify invasive species
 823 into 15 forms of invasiveness based on combinations of high local abundance (A),
 824 broad environmental range (E), wide geographic range (G) and fast spread rates (S).
 825 Pie charts in each cell indicate the percentage of 112 studies that used those
 826 dimensions to identify invasive species as determined by the classification criteria
 827 reported or invoked in the studies (Table S4). Letters and colour-coded shading
 828 indicate cases where that dimension is explicitly used as a criterion of invasiveness
 829 (some colours overlap indicating use of multiple criteria, see Table 2), e.g. AEGS, all
 830 demographic dimensions are used as criteria. None: proportion of studies where none
 831 of the four demographic dimensions were used as criteria of invasiveness (8.0% of
 832 studies did not specify the criteria used). When impact was considered, 28 of the 31

833 forms of invasiveness were used in these 112 studies (no studies used only impact as a
834 criterion of invasiveness).

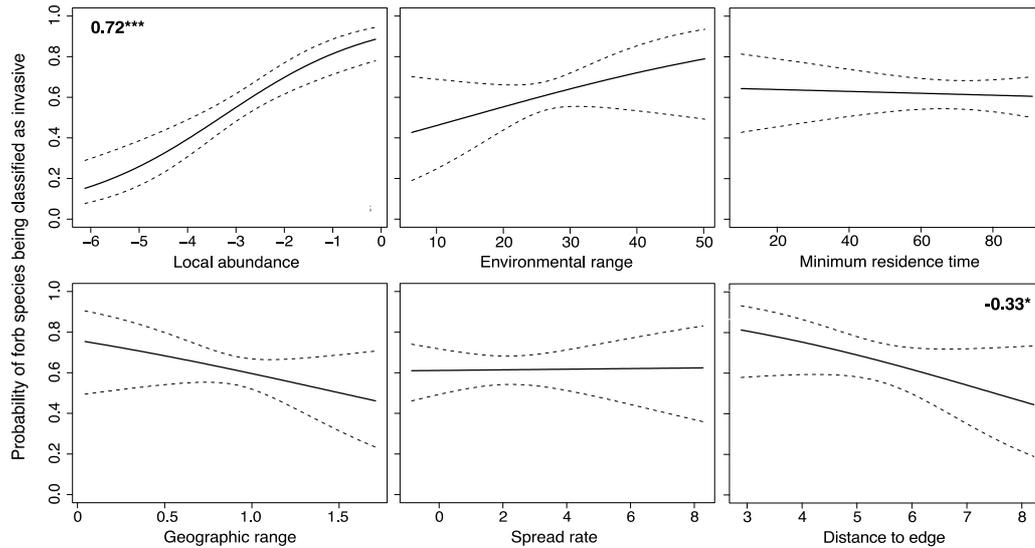
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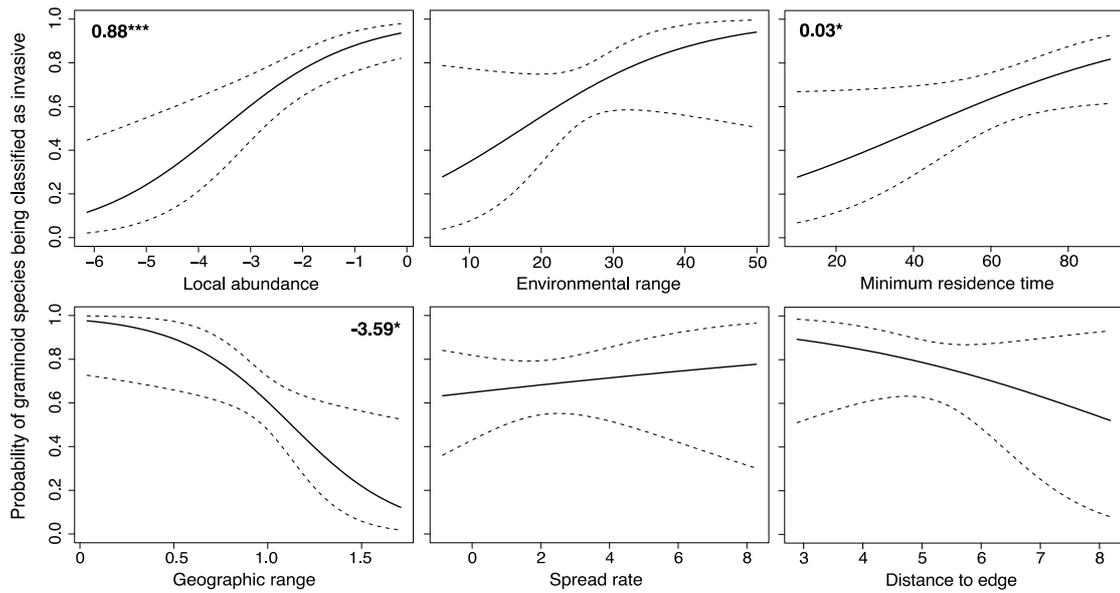
839 **Fig. 2.** Relationships among the four demographic dimensions of invasiveness for 340
 840 alien forbs and graminoids in Victoria. Pearson correlation coefficients are shown in
 841 each panel; $|r| > 0.5$ in bold font. Units of measurement: local abundance = log-
 842 transformed maximum relative cover observed in a quadrat; environmental range size
 843 = geometric mean of the standard deviations of four environmental variables in their
 844 original units (Appendix S1); geographic range size = geometric mean of the standard
 845 deviations of latitude and longitude (decimal degrees); spread rate = log-transformed
 846 rate of geographic spread (km/year). Invasive species in black circles, non-invasive
 847 species in white circles. Correlations with and among MRT and distance to edge were
 848 all $|r| < 0.5$ (Table S5).



849

850 **Fig. 3.** Predicted probability of 240 alien forbs being classified as invasive based on
 851 species' local abundance, environmental range size, geographic range size, spread
 852 rate, minimum residence time and distance to edge. Units of measurement: minimum
 853 residence time = years between first and last observation in Victoria for period 1900-
 854 1991 inclusive; distance to edge = log-transformed mean of distance to edge of
 855 vegetation fragments (km); others provided in caption of Fig. 2. Significant slope
 856 coefficients are reported; *** $p < 0.001$, * $p < 0.05$; dotted lines are 95% credible
 857 intervals.

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860 **Fig. 4.** Predicted probability of 100 alien graminoids being classified as invasive
 861 based on species' local abundance, environmental range size, geographic range size,
 862 spread rate, minimum residence time and distance to edge. Details as in Fig. 3.

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