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Author/s:

Catford, JA;Baumgartner, JB;Vesk, PA;White, M;Buckley, YM;McCarthy, MA

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Title: Disentangling the four demographic dimensions of species invasiveness

Jane A. Catford^{1,2,3*}, John B. Baumgartner^{1,4}, Peter A. Vesk¹, Matt White⁵, Yvonne M. Buckley⁶, and Michael A. McCarthy¹

¹School of BioSciences, The University of Melbourne, Vic 3010, Australia.

²Fenner School of Environment and Society, The Australian National University, Canberra, ACT 2601, Australia.

³Department of Ecology, Evolution and Behavior, University of Minnesota, Saint Paul, MN 55108, USA.

⁴Department of Biological Sciences, Macquarie University, NSW 2109, Australia.

⁵Arthur Rylah Institute for Environmental Research, Department of Environment, Land, Water & Planning, 123 Brown Street, Heidelberg, Vic 3084, Australia.

⁶School of Natural Sciences, Zoology, Trinity College Dublin, University of Dublin, Dublin 2, Ireland.

*Corresponding author: Jane A. Catford, School of BioSciences, The University of Melbourne, Vic 3010, Australia, Tel.: +61 2 6125 2286, Fax.: + 61 2 6125 0746, Email: catfordj@unimelb.edu.au

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Keywords: 15 demographic forms of invasiveness; invasive alien species; definition; impact; invasion ecology; functional traits; four demographic dimensions of invasiveness; non-native plants; Rabinowitz; review & synthesis

Type of article: Essay review **Summary**

1. A definitive list of invasive species traits remains elusive, perhaps due to inconsistent ways of identifying invasive species. Invasive species are typically identified using one or more of four demographic criteria (local abundance, geographic range, environmental range, spread rate), referred to here as the demographic dimensions of invasiveness.
2. In 112 studies comparing invasive and non-invasive plant traits, all 15 combinations of the four demographic dimensions were used to identify invasive species. 22% of studies identified invasive species solely by high abundance while 25% ignored abundance.
3. We used demographic data of 340 alien herbs classified as invasive or non-invasive in Victoria, Australia to test whether the demographic dimensions are independent and which dimensions influence invasive species listing in practice.
4. Species' abundances, spread rates and range sizes were independent. Relative abundance best explained the invasiveness classification. However, invasive and non-invasive species each spanned the full range of each demographic dimension, indicating that no dimension clearly separates invasive from non-invasive species.
5. Graminoids with longer minimum residence times were more frequently classified as invasive, as were forbs occurring near edges of native vegetation fragments.

Synthesis. Conflating multiple forms of invasiveness by not distinguishing invasive species that are identified using different demographic criteria may obscure traits possessed by particular subsets of invasive species. Traits promoting high abundance likely differ from those enabling fast spread and broad ranges. Examining traits linked with the four demographic dimensions of invasiveness will highlight species at risk of becoming dominant, spreading quickly or occupying large ranges.

Introduction

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

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

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

In order to determine whether the demographic dimensions are correlated, making some redundant in practice, we analysed correlations among the relative abundances, environmental and geographic range sizes, and spread rates of 340 "invasive" and

“non-invasive” alien (non-native, introduced) herbs in Victoria, Australia. Accounting for minimum residence time and habitat fragmentation, we find that the dimensions of invasiveness in this dataset are largely independent and that local abundance was the demographic dimension most strongly linked with this invasive species classification. Having demonstrated that species identified as invasive show many different demographic patterns and that no one demographic dimension clearly separates invasive from non-invasive species, we briefly present a few examples of plant traits that might relate to the demographic dimensions. We conclude by outlining a method to strengthen the understanding of traits that promote invasiveness. We focus on plants in this manuscript, but note that similar arguments may apply to other taxa.

Criteria that underpin definitions of invasiveness

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

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

122 Either implicit or explicit to the 43 definitions was the need for invasive species to
123 form self-sustaining populations beyond their natural range, which was usually
124 achieved via human introduction (Table S1). We did not include “the ability to form
125 self-sustaining populations” as a criterion of invasiveness because it does not
126 distinguish invasive alien species from alien species that are naturalised but non-
127 invasive. We regard invasiveness as an attribute, or characteristic, of a species.
128 Invasiveness is distinct from invasion success (Catford *et al.* 2012b), which is affected
129 by the abiotic characteristics of the invaded ecosystem, biotic interactions between the
130 invading and resident species, and propagule pressure of the invader (Catford, Jansson
131 & Nilsson 2009).

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

133 We note that impact is often used as a criterion to identify invasive species and thus
134 acts as a fifth dimension of invasiveness. However, we restrict our focus to the four
135 demographic dimensions in this paper. Our goal is to provide a framework for finding
136 traits that reliably and consistently predict invasiveness. Invasive species impacts
137 include a diverse range of negative ecological, economic, human health and aesthetic
138 impacts (Table S1), so impact itself could be characterised as multidimensional, with
139 relevant traits depending on the impact of concern. Identifying a common suite of
140 impact-related traits is therefore far less likely than identifying a suite of traits related
141 to the other four dimensions of invasiveness, which are more limited in scope.
142 Species’ overall impacts are partly determined by their abundance and distributions
143 such that the four demographic dimensions may suffice as indicators of impact.
144 Although species could potentially cause significant harm (and be considered
145 invasive) even if they have low abundance and small ranges, species are most likely
146 to be harmful when their abundances are high and range sizes large (Buckley &
147 Catford 2016). This is illustrated by Parker *et al.*’s (1999) model of invasive species
148 impacts where net impact is a function of species’ per capita effects, abundance and
149 geographic range size. Our focus on demography is consistent with some other studies
150 that focus on the ecological aspects of invasiveness (e.g. Ricciardi & Cohen 2007;
151 Wilson *et al.* 2009) (but see Vilà *et al.* 2011; Pyšek *et al.* 2012).

152 **Forms of invasiveness**

With the exception of spread rate, the demographic dimensions used to define invasiveness are the same dimensions used by Rabinowitz (1981) when defining species rarity. In her seminal work, Rabinowitz (1981) proposed seven forms of rarity based on combinations of species' local population size (local abundance), geographic distribution (geographic range size) and habitat specificity (environmental range size). Though some combinations may give rise to rare species more often than others (Rabinowitz 1981), she convincingly argues (and subsequently demonstrates, Rabinowitz, Cairns & Dillon 1986) that species can be rare in different ways.

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

Incorporating spread rates into Rabinowitz's scheme gives rise to 15 demographic forms of invasiveness ($2^4 - 1 = 15$, Table 2; including impact as the fifth dimension would result in $2^5 - 1 = 31$ forms of invasiveness). Although the demographic forms and demographic dimensions of invasiveness are related, the former result from different combinations of the latter (following Rabinowitz 1981), so they are distinct concepts (Table 2); we refer to both concepts throughout the paper. The most extreme demographic form of invasiveness would comprise invasive species that reach high local abundance and have broad geographic ranges, wide environmental ranges and fast spread rates (AEGS in Table 2). Although presented as distinct forms of invasiveness, it is important to note that the dimensions underlying these 15 forms are continuous and are not demarcated by thresholds that distinguish e.g. high abundance from low abundance. Thresholds may be found that enable categorisation, but it will likely be more informative to retain continuous dimensions in any trait-based analyses (see Discussion; Carboni *et al.* 2016).

We reviewed a sample of the trait-based invasion literature to determine whether all 15 forms of invasiveness are used to identify invasive species and whether a particular

form may be used more than others. Our sample consisted of 112 field or experimental-garden studies that compared the trait values of invasive alien species with non-invasive species, as used by van Kleunen et al. (2010) in their meta-analysis examining invasive species traits [we were unable to access 6 of the 118 papers used by van Kleunen et al. (2010)]. We chose this sample of papers because each of the studies specifically contrasted invasive and non-invasive species in an attempt to identify the traits that distinguish them and, as such, presumably had strong reasons for distinguishing the two types of species. Specific definitions of invasiveness were rarely presented in the 112 studies, but most authors stated their rationale for species selection; we used this information to represent the criteria used to distinguish invasive and non-invasive species (Table S2). Critically, even if a species was classified as being invasive based solely on its abundance, this does not necessarily mean that the species had slow spread rates or small ranges. Rather, it indicates that the other three demographic dimensions were not used as criteria of invasiveness (Table 2, Figure 1), so the species could be distributed anywhere along those dimensions (e.g. high, low or medium spread rates).

The 112 studies used all 15 demographic forms of invasiveness (Fig. 1, Table 2): all four demographic dimensions were used and some definitions shared no common criteria. If impact was included as the fifth dimension, 28 of 31 forms were used, but impact was never used as a criterion by itself (Table S2; 62% of the 112 studies did not use impact to identify invasive species, indicating that species can be considered invasive without necessarily having negative impacts). Of the four demographic dimensions, abundance was most commonly used (66% of studies) and 22% of studies identified invasive species solely on abundance. However, 25% of the 112 studies did not include abundance as a criterion (Fig. 1), meaning that the invasive species featured in these 28 studies could potentially occur at low abundances, in contrast to the species in 74 studies that must reach high local abundance. After abundance, geographic range size was the next most commonly used demographic criterion (44%), followed by spread rate (38%). Environmental range was the least used criterion (22% of studies). Eight studies did not document the rationale for species selection, and two studies referred to databases for lists of invasive species. A single criterion was used to identify invasive species more frequently than multiple criteria (36% of studies used one criterion), but 34% of studies relied on two criteria

(19% used three criteria; 3% used four criteria; 9% used none of the four demographic criteria).

Are the demographic dimensions of invasiveness independent in practice?

Our review of 112 studies illustrates that invasive species are identified in many ways using multiple criteria, indicating support for multiple dimensions of invasiveness. However, a single dimension may be used in practice, or the four demographic dimensions may be highly correlated such that abundant alien species are also those with fast spread rates, wide geographic ranges and broad environmental ranges. We assessed whether each of the four demographic dimensions of invasiveness was correlated with an invasive species classification using a case study of alien plant species in Victoria, a 237,629 km² state in south-eastern Australia.

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

Use of the existing Carr *et al.* classification allowed us to: 1) assess the independence of the demographic dimensions of invasiveness for a large suite of plant species and the likely existence of different forms of invasiveness; and 2) determine whether species’ demography (as represented by the demographic dimensions of invasiveness) relates to species’ (perceived) ecological impacts (as represented by the Carr *et al.* classification), as theory would predict (Buckley & Catford 2016). Being based on the

overall threat that alien species pose to native vegetation, which likely takes into account species' per capita effects plus demography, the Carr *et al.* scheme enabled us to avoid circularity that would stem from testing, for example, an abundance-based classification scheme using data on species' abundances.

We used plant occurrence and cover data for 2714 taxa that are alien (non-indigenous) to Victoria (149,772 presence records from 1900 through 1991 from Victoria's Flora Information System (FIS) and Australia's Virtual Herbarium; 19,057 abundance records from 1970 through 1991 from FIS, which were collected from areas not directly modified by intensive human land use; Appendix S1). Observations before 1900 were imprecise. We set the end date as 1991 so that the modeled data corresponded with information that would have informed the 1992 invasive species classification (Carr, Yugovic & Robinson 1992). We limited analyses to alien species that had at least 20 presence records and the necessary demographic data (391 species). Of these 391 species, Carr, Yugovic and Robinson (1992, p.15) had classified 259 of them as either: "not a threat (but may have a negative visual impact)" (14 species); "potentially serious threat to one or more vegetation formations" (72 species); "serious threat to one or more vegetation formations" (99 species); or "very serious threat to one or more vegetation formations" (74 species). The demographic characteristics (described below) of potentially serious, serious and very serious threat species were indistinguishable from each other, so we combined these three types of species into one category, which we call "invasive" (245 species). We assigned 132 unclassified alien species to the "not a threat" category, which we call "non-invasive" (146 species). Carr, Yugovic and Robinson (1992) considered all alien species naturalized in Victoria in their assessment, but restricted their classification to a subset of alien plants considered environmental weeds, which "invade native vegetation, usually adversely affecting survival of the indigenous flora" (p. 4). This indicates that unclassified taxa were not considered a threat to native vegetation and only differ from the 14 classified "no threat" species in that the latter may have a visual (but not ecological) impact; we are not concerned with aesthetics here.

Species' *local abundance* was represented by the maximum cover abundance of each taxon calculated as a proportion of summed species cover in 30 m × 30 m survey

plots. We use proportional cover, rather than absolute cover, because it accounts for variation in site productivity and the abundance of other species (Catford *et al.* 2012b), and accords with the way abundance is usually related to invasiveness in the literature (Table S2).

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

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

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

$$D_{it} = \text{asym}_i / (1 + \exp((\text{mid}_i - t) / \text{scal}_i))$$

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

In their assessments of alien species threat, Carr, Yugovic and Robinson (1992) may have accounted for the time available for populations of each species to grow and spread, or the strength of species' associations with anthropogenic habitats (e.g. they

may have down-weighted the risk of species that only occur at the edges of vegetation fragments and around human settlements). We therefore quantified minimum residence time (MRT) to account for time since introduction and distance to edge (akin to habitat fragmentation) to jointly account for variation in propagule pressure and human disturbance (Catford *et al.* 2011), which may facilitate invasion (Pyšek *et al.* 2015). MRT was calculated as the number of years between the first recorded observation (from 1900 onwards) in native-dominated vegetation in Victoria and 1992. For each species, we quantified the mean distance between each observation and the edge of the associated vegetation fragment (e.g. distance to road, distance to crops).

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

The probability that taxon i was classified as invasive was:

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

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

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

Results and discussion of the Victorian analysis

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

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

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

Contrary to expectations, the probability of a graminoid being classified as invasive (as opposed to non-invasive) decreased with increasing geographic range sizes. This may reflect an assessment by Carr, Yugovic and Robinson (1992) that graminoids with wide distributions posed less of a threat to native vegetation than graminoids with narrow distributions because the former had already filled most of their potential range and exerted their impacts. The negative relationship could also reflect our methodological approach, which restricted analyses to species with ≥ 20 observations. This threshold was essential for calculating representative range sizes, but also meant that non-invasive species, which are perhaps more likely to have small ranges than invasive species, were disproportionately excluded (78% of the graminoids and forbs with < 20 presence records were classified as non-invasive, whereas 41% of the species with ≥ 20 presences were classified as non-invasive).

Graminoids with longer minimum residence times were more likely to be classified as invasive than graminoids with shorter MRT (Fig. 4). There were no correlations between species demography and MRT, suggesting that, for graminoids, species introduced earlier may have been more likely to exert impacts (not assessed here). Alternatively, Carr *et al.* may have been more familiar with graminoids introduced

earlier than graminoids introduced later. Forbs classified as invasive were generally recorded closer to the edge of vegetation fragments than forbs classified as non-invasive. This was surprising, as alien species that invade intact native vegetation would presumably pose a greater threat to native plant species – the aim of Carr *et al.*'s classification. The greater visibility (and therefore familiarity to Carr *et al.*) of alien forbs at the edge of vegetation fragments (compared to alien forbs in the interior of fragments) may have affected the classification of these species.

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

Although we found that species abundance was correlated with Carr *et al.*'s threat-based classification, we also highlight that some species can be listed as invasive for reasons that are unrelated to their observed demography. *Eragrostis curvula* (Schrad.) Nees is classified as invasive in Victoria despite being ranked 99th for relative abundance, 86th for environmental range, 67th for geographic range and 81st for spread rate out of 100 invasive and non-invasive graminoids. Its classification may reflect high per capita effects, which may result in this species reaching a high threat status despite its seemingly benign demography. The classification of *E. curvula* as invasive may also reflect evidence of its invasiveness elsewhere, or that the abundance data were collected from plots used to characterize native vegetation and thus are not a random sample of Victoria's vegetation.

The Victorian analysis illustrates that species are classified as invasive for different reasons and invasive species can exhibit several distinct demographic characteristics. Apart from geographic and environmental range size, the dimensions were independent of each other, indicating that three of the four demographic dimensions inform this invasive species listing and that multiple forms of invasiveness exist in Victoria. Local abundance was the main predictor of the classification, but some forbs and graminoids were classified as invasive for reasons other than their abundance. If searching for traits related to invasive forbs and graminoids in Victoria, it would

therefore be worthwhile distinguishing among these different forms of invasiveness by examining traits related to three of the demographic dimensions (because of their strong correlation, it would only be necessary to examine traits related to geographic range size or environmental range size, not both).

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

Discussion

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

Demographic dimensions of invasiveness may be associated with different functional traits

Based on current ecological understanding, it seems likely that the functional traits related to the four demographic dimensions differ. We briefly note a few examples. By helping populations grow from a small size, self-compatibility (Lovett-Doust 1981) and clonality (Rejmánek 2011) should facilitate high local abundance and fast spread rates, but these traits should be less important for range sizes. The ability to disperse long distances should be crucial for achieving fast spread and wide

geographic range sizes (Nathan *et al.* 2008), but should not facilitate high local abundance or broad environmental ranges. High phenotypic plasticity, genetic polymorphism and outcrossing can increase intraspecific variation and should therefore facilitate broad environmental ranges (Sultan 2001; Pohlman *et al.* 2005; Rejmánek 2011). These three traits may be indirectly related to geographic range because of correlations between environmental and geographic range sizes, but they are unlikely to correlate with local abundance and spread rate.

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

Potential implications of conflating demographic dimensions

Current understanding suggests that plant traits relate to local abundance, spread rate, and geographic and environmental range sizes in different and sometimes contrasting ways. If studies identify invasive species using different demographic dimensions, it may therefore be hard to ascertain the functional traits associated with invasiveness. Though it would be undesirable if trends were rendered weak, uncertain or inconsistent because of this issue, a greater concern is that traits might be overlooked altogether, despite being strongly related to a dimension of invasiveness. Below, we outline four main ways in which conflating dimensions may obscure trait-based trends.

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

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

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

Some traits may relate to multiple dimensions of invasiveness because dimensions may share underlying population characteristics (e.g. long-distance dispersal should be positively linked with both spread rate and geographic range size), or because of life history tradeoffs and phylogenetic conservatism (van Kleunen, Weber & Fischer 2010). Although traits that have a consistent interpretation across multiple dimensions of invasiveness would make robust indicators, there are many cases where contradictory trait-based trends seem likely (e.g. traits related to colonisation versus competitive ability, and habitat generalists versus habitat specialists, noted above). The way to interpret some traits is even unclear within a single dimension. Having many, light seeds can facilitate high local abundance by increasing the probability of arriving in a safe site suitable for germination, but seedlings from large seeds have a higher probability of establishing in any given site (Muller-Landau 2010). Also within the abundance dimension, traits associated with high abundance in disturbed ecosystems are often in contrast to those associated with high abundance in undisturbed ecosystems (Tilman 1982; van Kleunen, Weber & Fischer 2010). Without knowledge of the local conditions for invasion, it is unclear how to interpret effects of seed mass and “coloniser” traits on species’ local abundance because of tradeoffs

between seed size and seed number, and tradeoffs between species' colonisation and competitive abilities.

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

To find trait-based trends that relate to the demographic dimensions of interest, invasive and non-invasive species must be identified using the same criteria, albeit representing different ends of the spectra. Some native species can have similar demographic characteristics to invasive alien species [both may be spreading (Thompson, Hodgson & Rich 1995), abundant (Firn *et al.* 2011) or common (Dawson, Fischer & van Kleunen 2012)], so invasive alien species should not simply be compared with any native species. Acknowledging this, many comparative studies exclude native species that are known to be invasive elsewhere (van Kleunen, Weber & Fischer 2010). However, rather than relying on criteria reported in invasive species definitions, it would be much more reliable to identify suitable study species using data about their abundance, spread rate and range sizes.

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

d) Rationale for invasive species listing is inaccurate or imprecise

Invasive species classifications commonly use expert-opinion derived from observation (Burgman 2004; McGeoch *et al.* 2012; Speek *et al.* 2013). Even if precise definitions are provided, people may be unaware of their own underlying motivations for listing some species as invasive because of cognitive biases (Burgman 2001; Hulme 2012). For example, a researcher may believe that they have classified a species as invasive because of its ability to spread rapidly, but this perception may in fact be the result of the species reaching high abundance over a large geographic range. Many authors do not provide specific definitions of invasiveness, instead providing broad definitions that encompass several options (Burgman 2001; McGeoch *et al.* 2012). As a consequence, even species (seemingly) identified using

the same criteria may be incomparable. Using empirical data, like in the Victorian analysis above, avoids the potential problems of expert-derived classifications.

A way forward

a) Focusing on the demographic dimensions of invasiveness

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

b) The importance of a comprehensive approach

It is important to account for propagule pressure, time since introduction, environmental conditions and characteristics of the recipient community when assessing invasiveness traits as these factors can affect invasion success (Wilson *et al.* 2007; Catford, Jansson & Nilsson 2009; van Kleunen, Weber & Fischer 2010; Rejmánek 2011; Gallagher, Randall & Leishman 2015; Pyšek *et al.* 2015). For example, the range sizes and abundance of species will be sensitive to the amount of time that species have had to invade. Despite a growing body of research (Ordonez, Wright & Olff 2010; Tingley *et al.* 2014; Pyšek *et al.* 2015), the combined influence of these factors is rarely examined in trait-based studies of invasiveness. To illustrate, at least 76% of the invasive species included in the 112 studies were associated with humans (1% not associated, 23% association not reported), in contrast to only 8% of the non-invasive species (18% not associated, 74% association not reported), yet only one study explicitly accounted for species' human association in their analyses (i.e. Grotkopp, Erskine-Ogden & Rejmánek 2010, Table S2). A strong association with humans through widespread planting and dispersal, for example, may elevate the

propagule pressure of certain species (Catford *et al.* 2012a), disentangling the relationship between their ecophysiological traits and their demography. Completely separating human- and species-mediated propagule pressure is likely to be difficult (Colautti, Grigorovich & MacIsaac 2006), but including a covariate that represents the strength of human association in analytical models should help (Wilson *et al.* 2007).

c) An analytical approach that offers greater nuance

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

d) Attributes of good indicators

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

Conclusion

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

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Data Accessibility

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

Supporting Information

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

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

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

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

Table S4: Results of logistic regressions that model the relationship between the probability of alien herbs being listed as invasive in Victoria and their local abundance, environmental range size, geographic range size, spread rate, minimum residence time and mean distance to edge: a) forbs (n = 240) and b) graminoids (n = 100).

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820 **Table 1.** The four demographic dimensions of invasiveness with examples of definitions that use them as criteria (underlined), ways in which
 821 they can be quantified, possible indicators and measures, and some potential management implications of focusing on a given dimension when
 822 designating species as invasive. As well as the indicators and measures listed here, we provide other examples of potential measures in the case
 823 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 strong impacts on native species” (Lankau <i>et al.</i> 2009, p. 15362).	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; density.	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 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

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 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).	Range or standard deviation of latitude and longitude; areal extent of occupancy .	populations that contribute more to spread (Epanchin-Niell & Hastings 2010). 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 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	“Invasive (E): Fully invasive species, with	Species' environmental range sizes can be characterised through	Number of habitat types a	Management would target species that occur across a broad range of environmental conditions and habitat

	a taxon resides. Proxies include species' latitudinal or altitudinal range or the number and diversity of habitat and ecosystem types that species occupy. The dimension least referred to in definitions of invasiveness.	individuals dispersing, surviving and reproducing at multiple sites <u>across a greater or lesser spectrum of habitats</u> and extent of occurrence" (Blackburn et al. 2011, p. 337).	species distribution modelling or by the diversity of habitats that species occupy.	species occupies; range of environmental conditions.	types. The efficacy of invasive species detection and management can vary depending on the environmental conditions of the invaded area, like terrain 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 definitions do not	"Alien species were designated as invasive if there	The most challenging demographic metric to quantify, requiring information about where	Distance a species' range front increases	Targets rapidly expanding populations. Early detection and intervention presents the best chance of containing species before geographic range and number of

specify actual spread rates, instead describing invasive populations as those that spread or those that spread rapidly.	was... <u>rapid range expansion or population growth in the introduced country</u> ” (McGeoch et al. 2010, p. 1 of Appendix S3).	and when species were introduced and records of how they have moved across the landscape. Many modelling approaches are available (Wilson <i>et al.</i> 2007; Andrew & Ustin 2010; Caplat, Nathan & Buckley 2012).	over a specific period of time.	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 <i>et al.</i> 2016).
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Table 2 A typology of 15 forms of invasiveness based on combinations of the four demographic dimensions: high local abundance (A), broad environmental range (E), wide geographic range (G) and fast spread rate (S). Adapted from Rabinowitz (1981). Adding the fifth dimension, 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.
	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.
Not used	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	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

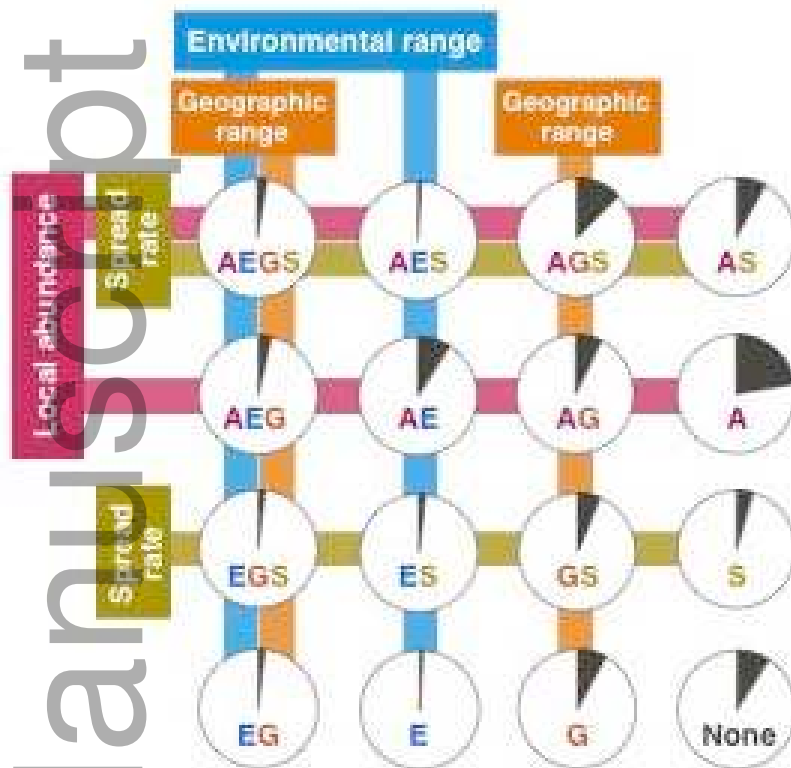
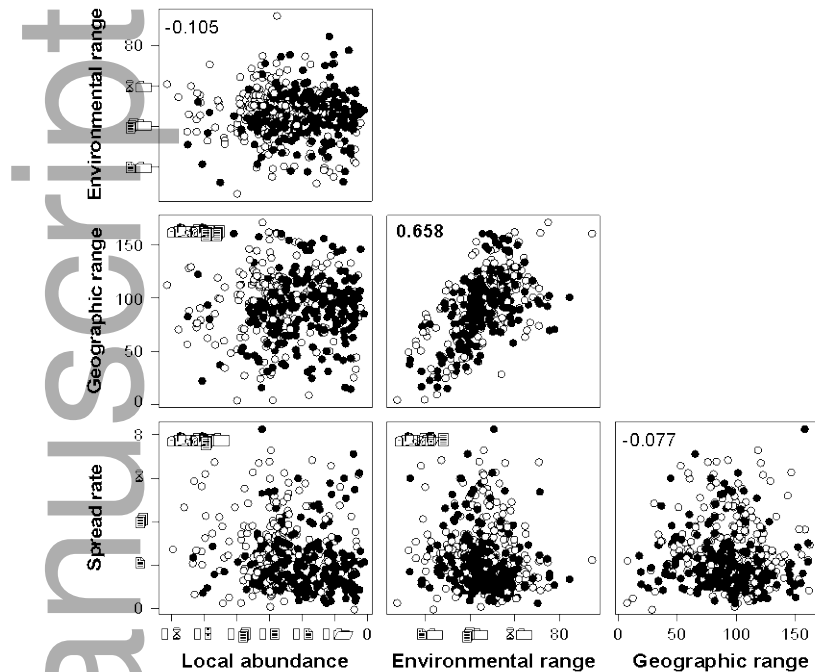


Fig. 1. Proportion of 112 trait-based invasion studies that classify invasive species into 15 forms of invasiveness based on combinations of high local abundance (A), broad environmental range (E), wide geographic range (G) and fast spread rates (S). Pie charts in each cell indicate the percentage of 112 studies that used those dimensions to identify invasive species as determined by the classification criteria reported or invoked in the studies (Table S4). Letters and colour-coded shading indicate cases where that dimension is explicitly used as a criterion of invasiveness (some colours overlap indicating use of multiple criteria, see Table 2), e.g. AEGS, all demographic dimensions are used as criteria. None: proportion of studies where none of the four demographic dimensions were used as criteria of invasiveness (8.0% of studies did not specify the criteria used). When impact was considered, 28 of the 31 forms of invasiveness were used in these 112 studies (no studies used only impact as a criterion of invasiveness).



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846

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

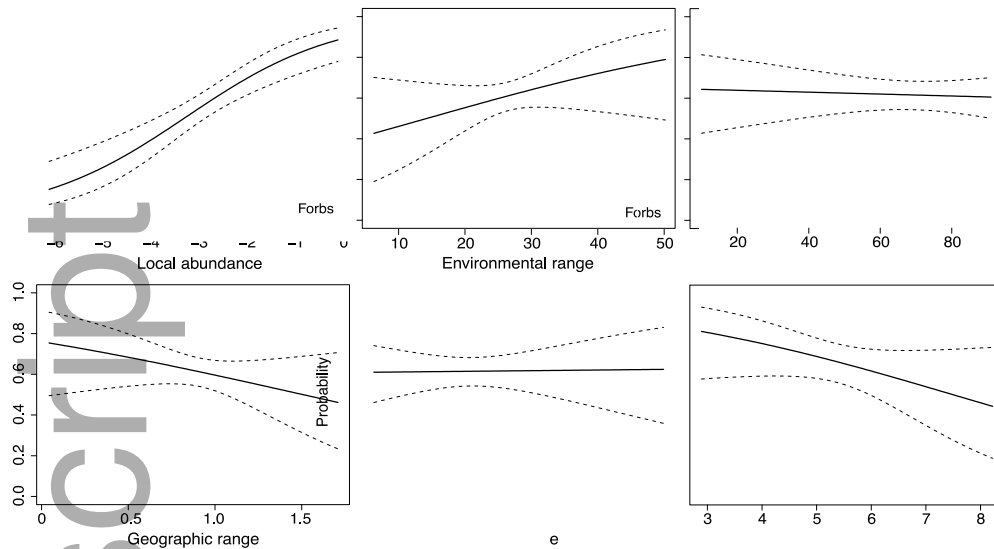
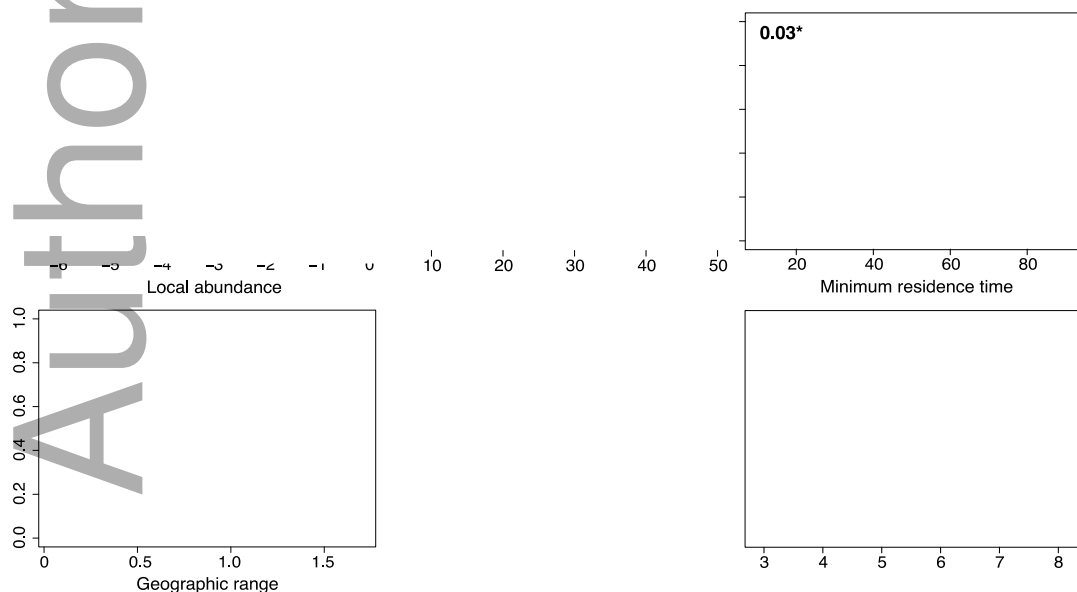


Fig. 3. Predicted probability of 240 alien forbs being classified as invasive based on species' local abundance, environmental range size, geographic range size, spread rate, minimum residence time and distance to edge. Units of measurement: minimum residence time = years between first and last observation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



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

Combinations of the demographic dimensions of invasiveness

