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DR. ESTIBALIZ PALMA (Orcid ID : 0000-0002-4500-254X)

DR. JANE A. CATFORD (Orcid ID : 0000-0003-0582-5960)

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AUTHORS

Estibaliz Palma,[1, 5] Peter A. Vesk,[1] Matt White,[2] John B. Baumgartner,[3] and Jane A.Catford[4]

[1]School of BioSciences, The University of Melbourne, Australia

[2]Department of Environment, Land, Water and Planning, Arthur Rylah Institute for Environmental Research, Australia

[3]Centre of Excellence for Biosecurity Risk Analysis (CEBRA), The University of Melbourne, Australia

[4]Department of Geography, King's College London, UK; School of BioSciences, The University of Melbourne, Australia

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[5]Corresponding author. E-mail: estibaliz.palma@gmail.com

ABSTRACT

Trait-based invasiveness studies typically categorize exotic species as invasive or non-invasive, implicitly assuming species form two homogenous groups. However, species can become invasive in different ways (e.g. high abundance, fast spread), likely relying on different functional traits to do so. As such, binary classification may obscure traits associated with invasiveness. We tested whether: (1) the way invasiveness is quantified influences its correlation with functional traits; and (2) different demography-based metrics are better explained by different sets of traits. Using a case study of 251 herbs exotic to Victoria, Australia, we quantified species' invasiveness using 10 metrics – four continuous, demography-based dimensions of invasiveness (spread rate, local abundance, geographic and environmental range sizes) and six binary classifications of invasiveness (based on alternative sources and invasion criteria). We examined the correlation between species' invasiveness and a set of four traits known to relate to plant demography and invasion. Then, we examined whether different demographic dimensions of invasiveness were better explained by different sets of traits. We found that the way invasiveness was quantified was important: different traits explained each invasiveness metric, and some traits showed opposite effects across metrics. Species with fast spread were either tall with small seeds (i.e. good colonizers), or had heavy, animal-dispersed seeds. Plants with large environmental range had greater plasticity for some traits. Locally abundant plants had low SLA and heavy seeds (i.e. strong competitors). Animal dispersal was also key to reach large geographic range. No traits were consistently related to the six binary classifications. Our results indicate that exotic plants are invasive in different ways and rely on different combinations of traits to do so. Some traits (e.g. seed mass) had complex relationships with invasion: they promoted, hampered or had no influence on different dimensions of invasiveness. Our findings are consistent with the notion that plant species use strategies which may be near-optimal under some, but not all, ecological conditions. Compared to binary classifications of invasiveness, the use of invasiveness dimensions advances clearer hypothesis-testing in invasion science.

KEYWORDS

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Demography metrics; Dimensions of invasiveness; Environmental and geographic range sizes; Exotic plant invasion; Invasiveness and invasive species; Local abundance; Plant functional traits; Spread rate

INTRODUCTION

Understanding how functional traits relate to invasion is key for understanding the mechanisms of biological invasion (Rejmánek 2011) and for predicting species that are likely to become invasive. Many studies have examined relationships between species' functional traits and invasion success (Sol et al. 2012, Gallagher et al. 2015, Carboni et al. 2016, Allen et al. 2017). However, despite a considerable research effort spanning multiple taxa, universal relationships between traits and species invasiveness remain unclear.

The meaning of "species' invasiveness" varies across contexts, reflecting the multiple, simultaneous causes that contribute to invasion. One way to gain clarity and improve a mechanistic understanding of invasiveness, is to focus on the demographic processes that promote invasion success - i.e. species growth, reproduction and spread (Richardson et al. 2000). Demography-based metrics of invasiveness reflect the continuous nature of plants' invasive ability and can serve to isolate particular invasion mechanisms. Plant invasiveness can be quantified through combined population performance measures (Colautti et al. 2014) and individual metrics of population size, frequency of occurrence, local abundance, spread rate, geographic range and niche breath (Moravcová et al. 2015, Carboni et al. 2016, Catford et al. 2016, McGeoch and Latombe 2016, Klinerová et al. 2018). These different metrics reflect the fact that plants are able to invade vegetation in various ways, likely relying on different traits to do so (Speek et al. 2011, Lai et al. 2015).

Most trait-based studies of invasiveness still examine differences between two discrete groups of species – broadly referred to as invasive and non-invasive. In the last decade alone, at least 22 trait-based, multi-taxa studies have been published that rely on binary classifications to quantify invasiveness-traits relationships (Appendix S1: Section S1). Determining whether a species belongs to either the invasive or non-invasive group can be challenging, and usually requires some degree of subjective judgement by experts. Regional lists of currently or potentially harmful species compiled by government scientists, managers, practitioners or other experts, such as Black and Grey Lists of alien species in the Czech Republic (Pergl et al. 2016), or DAISIE and EASIN databases in Europe (Katsanevakis et al. 2015), are often used as the basis

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for binary classifications. Because binary classifications do not distinguish among species that are invasive in different ways and to different degrees, much information about species invasiveness is effectively omitted from these studies, limiting the inferences that can be made. Building on research by Catford et al. (2016), in this paper we focus on four continuous, demography-based dimensions of invasiveness: spread rate, environmental and geographic range sizes and relative local abundance (i.e. dominance). These demographic dimensions are commonly alluded to (and potentially conflated) by using invasiveness criteria that simultaneously consider species' ability to produce reproductive offspring, quickly disperse to areas far from the point of introduction and establish populations in undisturbed plant communities (Richardson et al. 2000, Blackburn et al. 2011). While spread rate, environmental range size and local abundance have a clear demographic nature, geographic range size is the composite result of dispersal dynamics and landscape configuration (i.e. spatial availability of suitable habitat patches). Although its interpretation may present some challenges, we still consider geographic range size in this analysis due to its widespread use as an invasiveness criterion (Catford et al. 2016). We ask:

1) do demographic dimensions of invasiveness and traditional binary classifications of invasiveness correlate differently with a specific set of functional traits?

2) are different demographic dimensions of invasiveness better explained by different sets of functional traits?

We expect the four demographic dimensions of invasiveness to relate to traits in different ways (Table 1), as summarised below.

Research from community and functional ecology suggests that smaller seed mass, which is linked to higher plant fecundity, will likely promote plants' spread rate and geographic range size (Moles and Westoby 2006) but will have a limited effect on environmental range size and a context-dependent effect on local abundance (Fig. 1). Dispersal distance tends to be greater for taller plant species (Thomson et al. 2011) and greater for species using animal dispersal compared to wind dispersal (Nathan et al. 2008), so these species will likely have larger geographic ranges and faster rates of spread. Heavy-seeded plants have lower fecundity and, therefore, fewer dispersal opportunities (Moles and Westoby (2006), but see Moles (2018)), which can slow their rate of spread (Fig. 1). However, heavy seeded species experience higher seedling establishment, especially under environmental hazards (Muller-Landau 2010), which

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may facilitate high relative abundance, especially when coupled with longer lifespans (Moles 2018). Plants with the ability to reproduce both sexually and asexually are expected to show greater relative abundance and spread rate (by fostering population growth and survival), and environmental range size (by broadening the ecological conditions under which the species can produce new individuals) (North et al. 2011). Species with fast leaf economics (Reich 2014), indicated by high specific leaf area, have higher population growth rates and reach reproductive maturity earlier, facilitating fast spread rates (Fig. 1). However, species with slow leaf economics are expected to be strong competitors and reach high relative abundance in undisturbed sites (Catford et al. 2019). When light is limiting, tall species are stronger competitors and will likely be more abundant than short species (Falster and Westoby 2003). Finally, phenotypic variability enables plants to cope with environmental heterogeneity (Menzel et al. 2017) and presumably survive under a wider range of environments (Fig. 1).

Addressing our two research questions, we first investigate whether the relationships between a set of four traits and invasiveness vary depending on the metrics used to characterise invasiveness, using a case study of 251 exotic herbaceous species in Victoria, Australia (Question 1). We used 10 metrics of invasiveness: four continuous, demography-based dimensions of invasiveness (spread rate, local abundance, geographic and environmental range sizes) and six binary (invasive/non-invasive) invasiveness classifications. Given that earlier introduced species have had more opportunities to become invasive (Castro et al. 2005), in addition to traits, we also consider species' minimum residence time. To address Question 2, we examine relationships between each of the demographic dimensions and a specific set of traits – selected based on their expected influence on one or more demographic dimensions (Table 1, Fig. 1). Our findings suggest that use of demographic dimensions of invasiveness has the potential to improve understanding of how traits relate to plant invasion.

MATERIALS AND METHODS

Study site and species records

Victoria is located in south-east Australia covering around 230,000 km^2. Home to over 6 million people, Victoria's climate ranges from cool and wet on the east coast to warm and dry in the north-west. The first records of exotic plants in Victoria date from the second half of the 18th

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century. By 2018, more than 1,780 exotic plant taxa were recognised as naturalized in the state (White et al. 2018).

A total of 431 exotic forb and grass species naturalized in Victoria have sufficient data to reliably estimate all four demographic dimensions of invasiveness (presented in Catford et al. (2016)). Records of species' occurrence, geographic location and time of detection in Victoria were collected from the Victorian Biodiversity Atlas and the Australasian Virtual Herbarium (AVH 2020) (details in Appendix S1: Section S2 and Catford et al. (2016)).

Traits and other covariates

We collected information on vegetative height, specific leaf area (SLA), seed mass, longevity ('annual or biennial'; 'perennial'), reproduction type ('sexual or asexual'; 'sexual and asexual'), seed morphology ('smooth'; 'hooked or fleshy') and dispersal vector ('wind'; 'other vector') for as many taxa as possible of these 431 exotic forbs and grasses found in Victoria. Height, SLA and seed mass were calculated using records available from the TRY (Kattge et al. 2020) and BIEN (http://bien.nceas.ucsb.edu/bien/) databases, complemented by measurements taken in Victoria by the authors (Appendix S1: Section S3). Using the combined records from online databases and Victoria, species-level variability for height and SLA was estimated through hierarchical models (Appendix S1: Section S3). Assuming species were random effects, the estimated standard deviation of each trait was used as an approximation for species' variability. Longevity, reproduction type, seed morphology and dispersal vector were extracted from several sources (Table 1), including the TRY database, printed literature and online resources (Appendix S1: Section S3). Correlation among traits was generally low (Appendix S1: Fig. S1).

We collated both published and anecdotal information about whether species were deliberately introduced to Victoria or not (including for ornamental, agricultural and soil or coastal stabilisation) and whether the taxa have been (or are) subject to weed control effort across the state. Minimum residence time was calculated as the number of years since the first record of the taxon in Victoria, as registered by the Australasian Virtual Herbarium (AVH 2020). We expected these three factors to affect invasion patterns (Table 1).

Metrics of invasiveness

1. Four demographic dimensions of invasiveness

Spread rate was estimated as the maximum slope of a hierarchical sigmoid growth model, which was constructed using data describing geographic spread over time. We assumed the earliest

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observation of each taxon represented its source population, and calculated the time elapsed to subsequent observed individuals and the cumulative distance of dispersal based on those individuals' geographic position. Then, the cumulative distance was modelled following:

$\text{cumdist} \sim \text{dnorm}(\text{mu.dist}, \text{sd.dist}^{-2})$

$\text{mu.dist} = \text{Asym}_i / (1+\exp((\text{xmid}_i-\text{time})/\text{scal}_i))$

Taxa, represented by *i*, were assumed to be random effects. Asym is the asymptotic spread of *i*; xmid is the time elapsed between taxon *i* reaching half of its asymptotic spread and its first observation; scal is the time elapsed between taxon *i* reaching half and about a third of its asymptotic spread; time represents the time elapsed between a given observation and the earliest records for the taxon. This model was fitted in R under a Bayesian inference framework and using informative priors based on Catford et al. (2016). The maximum slope of the model was then calculated for each taxon as the gradient between asymptotic spread at the time the taxon had reached half the asymptotic spread (xmid) and the time it had reached about a third of the asymptotic spread (scal) (Appendix S1: Section S4).

Propagule pressure and propagule biases affect observed patterns of invasion (Simberloff 2009) and, when not accounted for, can obscure trait-based invasiveness studies (Colautti et al. 2006). Post-introduction human-mediated dispersal (e.g. attached to vehicles, contaminants in hay) has likely influenced the dispersal pattern of exotic species in Victoria (Dodd et al. 2015), but is unlikely to relate to typical dispersal traits of plants. To reduce the relative influence of human-mediated dispersal in species' spread patterns we penalised spread rate (Appendix S1: Section S5) when individuals were found within a kilometre of land use other than natural vegetation (Catford et al. 2011). This penalty sought to minimise the influence of areas with high levels of exotic species' occupancy stemming directly from human-mediated movements (Colautti et al. 2006) and, therefore, the contribution that human-driven landscape dispersal may have on patterns of species distribution. Penalising in this way should more accurately reflect the natural dispersal ability of plants, which should be linked with the traits we examine in this work.

Environmental range size was estimated as the geometric mean of the standard deviation of uncorrelated environmental variables – maximum temperature in the warmest quarter, precipitation in the coldest quarter, soil radiometric thorium concentration and topographic wetness index – at locations where the taxon was detected. From the range of environmental information available through the Victorian Biodiversity Atlas, these four variables have been

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previously found to best explain exotic plants' occurrence across the sampled plots (Catford et al. 2011).

Geographic range size was estimated as the geometric mean of the standard deviation of the latitude and longitude of the locations where the taxon was recorded across Victoria. Standard deviations were used instead of more common approaches, such as latitude/longitude range or convex hulls, because they are not affected by potential differences in sampling effort (Burgman 1989).

Local abundance was defined as the observed maximum relative cover of each taxon across the network of survey plots (Victorian Biodiversity Atlas). As such, this indicates local dominance. Correlation among dimensions was low (Appendix S1: Fig. S2).

2. Six binary metrics of invasiveness

The 251species with records for SLA, height, seed mass and reproductive type were classified as invasive or non-invasive (Appendix S1: Table S1) according to four invasiveness classification schemes, each of which relies on different underlying criteria and motivations (Table 2, Appendix S1: Section S6). In two cases, the same ordinal scheme was used to create two different binary classifications following more strict or relaxed criteria, with the aim of exploring the effect of the subjectivity associated with definitions of invasiveness (Table 2).

Classification I - Noxious: The List of Declared Noxious Weeds in Victoria lists exotic species that legally must be managed in the state [resulting in 27 invasive; 224 non-invasive].

Classification II - Literature: invasion status of all plants introduced to Australia based on the literature (Randall 2007) [50 invasive; 201 non-invasive].

Classifications III and *IV - Expert opinion inclusive* and *Expert opinion limited:* Re-evaluation of the list of Environmental Weeds of Victoria (Carr et al. 1992), adding the species not included in the original publication due to their recent introduction to Victoria (by G. Carr, pers. comm., April 13, 2016 and December 7, 2017). Depending on whether species listed as 'potential threats' were categorized as invasive or non-invasive, we derived two binary classifications: *Expert opinion inclusive* [205 invasive; 46 non-invasive] and *Expert opinion limited* [102 invasive; 149 non-invasive].

Classifications V and *VI - Semi-quantitative inclusive* and *Semi-quantitative limited:* Rank of environmental weeds in Victoria following the perceived risk they pose to native ecosystems (White et al. 2018). The rank provides a prioritisation of management urgency based solely on

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ecological criteria. Again, depending on whether ’medium’ and ’moderately high’ risk weeds were considered invasive or non-invasive, we derived two binary classifications: *Semi-quantitative inclusive* [233 invasive; 18 non-invasive] and *Semi-quantitative limited* [88 invasive; 163 non-invasive].

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Statistical analyses

Question 1: Differences among the 10 metrics of invasiveness

We fit independent linear models to the four demographic dimensions of invasiveness and the six binary classifications of invasive plants. For all these models, we chose a small group of explanatory covariates widely used across invasiveness studies, including four traits (height, SLA, seed mass and reproduction type) and minimum residence time. The model structure was constant across the 10 response variables (metrics of invasiveness). We selected covariates most likely to capture the range of ways in which species can be invasive (Table 1).

For each demographic dimension of invasiveness, the model followed the form:

$Y_i \sim \text{Normal}(\text{mean}_i, \text{sd}_i)$

$\text{mean}_i = \alpha + \sum (\beta_t * x_{it})$

where Y is the value of the invasiveness dimension for species *i*, and its mean varies as a function of trait *t*, with x_{it} being the value of trait *t* for species *i*. The four demographic dimensions were standardized prior to model fitting to allow cross-comparison of trait effects and improve model convergence. Spread rate and local abundance were previously log- and logit-transformed, respectively.

For each binary classification of invasiveness, the model followed the form:

$Y_i \sim \text{Bernoulli}(p_i)$

$\text{logit}(p_i) = \alpha + \sum (\beta_t * x_{it})$

where Y is the assigned invasive/non-invasive state of species *i*. The probability of being classified as an invader, p, varies as a function of trait *t,* with x_{it} being the value of trait *t* for species *i*.

Continuous traits were log-transformed to avoid skewed distributions and standardized to facilitate the comparison among effects (Gelman and Hill 2007). Traits were considered to affect invasiveness when the 95% credible intervals of the associated parameter β did not overlap zero. We used visual comparison to assess similarities among models that were based on different invasiveness metrics. Invasiveness metrics that characterise species’ invasiveness in a similar

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way (e.g. focusing on the same demographic dimension or general criteria) are expected to show similar trends in their correlation with the traits under examination. We ran a parallel set of models to determine the relationship between the binary classifications of invasiveness (as response variables) and the demographic dimensions of invasiveness (as the explanatory variables).

Question 2: Traits and demographic dimensions of invasiveness

For the four demographic dimensions of invasiveness, we built a second group of independent linear models, this time using a different set of traits as explanatory variables for each of the dimensions (Table 1). We followed a hypothesis-driven selection of traits, rather than a model selection approach. *A priori* selection of predictor variables based on previous knowledge has been found to improve model predictive capacity, at least for trait-based vegetation growth models (Thomas et al. 2019).

Models were specified as follows:

$Y_i \sim \text{Normal}(\text{mean}_i, \text{sd}_i)$

$\text{mean}_i = \alpha + \sum (\beta_t * x_{it})$

Invasiveness dimensions and continuous covariates were log- or logit-transformed, as for *Question 1*, and standardised. Trait *t* was considered to affect invasiveness when the 95% credible intervals of β did not overlap zero.

The selection of the species used for the analyses did not follow a phylogenetically stratified approach, and consequently some clades are better represented than others in the dataset. To remove the effect of phylogenetic correlation on species' invasiveness similarities, we built a phylogenetic distance matrix, based on Zanne et al. (2014), and used it to constrain the structure of the residuals in the models (Ives and Zhu 2006). Based on an examination of our data, we found no evidence that we needed to consider non-linear or unimodal relationships in any of our analyses (Appendix S1: Fig. S3).

All models were run from R through the R2jags package (Su and Yajima 2015) under a Bayesian inference framework that used minimally informative priors (Appendix S1: Section S7). All models converged. We calculated the Pearson's correlation coefficient (R^2) for all models.

RESULTS

Question 1: Evaluation of the 10 metrics of invasiveness with common explanatory traits

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In general, our results showed high variability in the relationships among different invasiveness metrics and traits (Fig. 2). Different invasiveness metrics were correlated with different sets of traits, and most traits showed positive, neutral and negative correlations across invasiveness metrics.

The direction and magnitude of the trait effects varied across binary classifications (Fig. 2a). Classifications with no clear ecological criteria (*I-Noxious*, *II-Literature*; Table 2) were correlated with lower SLA and with taller height, but showed no correlation with seed mass, ability to reproduce both sexually and asexually, or time since introduction. Classifications *III-Expert opinion inclusive* and *V-Semi-quantitative inclusive*, which were based on ecological criteria with an inclusive approach, were both correlated with lower SLA, but showed opposite correlations with height and no correlation with the other three covariates. Classifications *IV-Expert opinion limited* and *VI-Semi-quantitative limited*, which were based on ecological criteria with a more restricted approach to classify species as invasive, showed no correlation with height or SLA; however, they show positive correlation with plants' ability to reproduce both sexually and asexually. Additionally, classification *IV-Expert opinion limited* was positively correlated with seed mass and minimum residence time.

We also found high variability in the relationship between the examined traits and the demographic dimensions of invasiveness (Fig. 2b). Plants' height, seed mass and SLA each showed a clear correlation with a single dimension (i.e. height with local abundance, seed mass and SLA with environmental range size), while reproduction type showed a correlation, yet in opposite directions, with multiple dimensions (i.e. environmental and geographic range sizes). Minimum residence time had a positive relationship with geographic range size but a negative relationship with spread rate. None of the invasiveness dimensions showed trends similar to those from any of the binary classifications, despite the fact that the *Semi-quantitative* and *Expert opinion* classifications include ecological criteria (Table 2). Models using the invasiveness dimensions as explanatory variables for the binary classifications models did not consistently explain more variation than those using traits as explanatory variables (Appendix S1: Table S2).

Question 2: Traits and dimensions of invasiveness

We found partial support for our expectations of how traits may promote or hamper multiple demographic dimensions of invasiveness (Table 1). Taller species and those with lighter seeds had faster spread rates (Fig. 3a). Species that had been deliberately introduced to Victoria and

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those with structural adaptations for dispersal by humans and other animals, especially if their seeds were heavier, had faster spread rates. Contrary to our expectations, we found that the ability to reproduce both sexually and asexually was negatively correlated with spread rate, and SLA had no effect on this dimension.

Plants with higher height variability had larger environmental ranges (Fig. 3b), but we found no consistent relationship between the size of plants' environmental range and their SLA variability, reproduction type or dispersal vector. Height variability and species' mean height were not correlated (R^2=0.12; Appendix S1: Fig. S1).

Contrary to our expectations, we did not find strong correlations between geographic range size and the evaluated traits, i.e. height, seed mass and seed morphology. However, we found that the interactions between seed mass and morphology had a positive effect, meaning that species with heavier seeds suitable for dispersal by animals had larger geographic ranges (Fig. 3c). Minimum residence time was also found to increase geographic range size.

We found that species with higher local abundance had heavier seeds and the ability to reproduce both sexually and asexually (Fig. 3d), but we found no consistent effect of height, longevity or management. There was some evidence that SLA was negatively related to local abundance, though this relationship was not statistically significant.

Models with specific sets of traits, selected individually for each demographic dimension (Fig. 3), did not explain more variance than models using a common set of traits (Fig. 2b). Differences found between the two sets of models (i.e. those related to Question 1 *vs* those related to Question 2; e.g. traits that correlate to spread rate, Fig 2b vs Fig. 3) likely reflect the different correlation structure behind the particular traits used for each model, and the use of a phylogenetic matrix in the models with specific sets of traits (Appendix S1: Table S3). Overall the explanatory power of the trait-based models was low (R^2<0.15). No patterns were observed on the models' residual plots (Appendix S1: Fig. S4).

DISCUSSION

By examining traits of hundreds of exotic herbaceous species that vary in the way that they are invasive, this study has shown that relationships between species' traits and invasiveness depend on how invasiveness is defined and quantified. Different trait-invasiveness relationships were found across 10 invasiveness metrics, including six binary classifications and four continuous, demography-based dimensions (Fig. 2). This finding indicates that herbaceous species can be

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invasive in different ways (e.g. occupying large areas or being locally dominant; Catford et al. (2016)), and developing simple demographic criteria to represent their invasiveness would benefit trait-based invasiveness studies and promote clearer hypothesis-testing in invasion science (McGeoch et al. 2012). We found that height, SLA, seed mass and reproductive type had a complex relationship with invasion; they showed positive, negative or no relationship across different invasiveness dimensions (Fig. 3). This finding is consistent with the existence of a diversity of life histories and functional strategies that confer invasion success under different contexts and ecological conditions (Dawson et al. 2009, Speek et al. 2011, Lai et al. 2015, Carboni et al. 2016, Shiflett et al. 2017, Catford et al. 2019).

Differences among the 10 metrics of invasiveness

We found no consistent relationships with traits across 10 invasiveness metrics (Fig. 2), which presumably reflects the diversity of invasiveness definitions (Catford et al. 2016) and the subjectivity and uncertainty associated with invasive species listing (McGeoch et al. 2012); this lack of consistency was apparent even between binary metrics based on the same classification scheme (e.g. *V-Semi-quantitative inclusive* vs. *VI-Semi-quantitative limited*; Table 2). A more detailed exploration of the relationship between traits and four demographic dimensions of invasiveness further revealed that different traits relate to different demographic processes (Fig. 3).

It is likely that binary classifications simultaneously consider multiple demographic criteria to determine species' invasiveness, and they may also consider species' realised or potential impact on either natural systems, agricultural systems or both. For example, the ranking process devised for White et al. (2018) promoted species on their unrealised potential to degrade natural systems. In this schema, recently naturalised perennial plants with the capacity to rapidly invade natural systems and aggressively compete with native species such as *Pilosella* spp. were considered more serious than already well-established and widespread, invasive plants with ruderal life-histories such as *Sonchus* spp. Condensing something as multifaceted as species invasiveness into two, or a few, categories could result in a highly heterogeneous group of "invasive species", a collection of species that are invasive in different ways. We found differences among the binary classifications based on non-ecological criteria (*I* and *II),* classifications with ecological and more inclusive criteria *(III* and *V*), and classifications with ecological and more restricted criteria for invasiveness (*IV* and *VI*) (Appendix S1: Section 6). These three classification groups

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correlated with traits in different ways (Fig. 2a). The first group (classifications *I* and *II*) considers taller plants and plants with low SLA as more invasive. These classifications are either focussed on economically important waterway or agricultural weeds (noxious weed listings) or reliant on publication (including noxious weed listings) hence a likely bias toward weeds of economic importance. The second group (classifications *III* and *V*), which uses ecological criteria, considers lower SLA species as invasive, suggesting that species' competitive ability under low resource availability is important. However, in the third group, when only highly invasive species are considered (classifications *IV* and *VI*), importance of height and SLA disappears, and reproductive ability and seed mass become more important. The differences between the last two groups (*inclusive* vs *limited*) at least in part reflects the motivations for ranking and listing. While species capable to ostensibly invade undisturbed natural ecosystems are classified as invasive in both *III-Expert opinion inclusive* and *V-Semi-quantitative inclusive* classifications ('potential threat' and 'moderate risk'; Table 2), Carr et al. (1992) and White et al. (2018) have a slightly different approach to decide which species are classified as their top invaders (*IV-Expert opinion limited* and *VI-Semi-quantitative limited*). While original categories 'serious threat' and 'very serious threat' in Carr et al. (1992) (binary classification *IV*) are based on the degree of impact on natural systems alone without consideration of past or future impact, original categories 'high risk' and 'very high risk' in White et al. (2018) (binary classification *VI*) are based on the magnitude of unrealised impacts on natural systems. Factoring species' impact into the invasiveness classification makes their link to functional traits even more difficult to disentangle, since impact – like demographic dynamics – is complex and may itself represent myriad processes that manifest in myriad ways (Ricciardi et al. 2013). Our findings suggest that functional studies of invasions would benefit from the additional accuracy, precision and transparency of information provided by demography-based metrics of invasiveness (van Kleunen et al. 2018).

Traits and demographic dimensions of invasiveness

We found that species with particular functional traits are more likely to achieve high levels of invasion through different demographic processes (Fig. 4). Taller species, and species with lighter seeds showed quick spread rates (Fig. 4a). These characteristics point to species of ruderal nature, with short lifespan and frequent dispersal opportunities, likely through wind (i.e. good colonizers). However, we found that species with heavier seeds can also achieve fast spread rates

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– likely due to long-distance dispersal events (Moles 2018) – when those seeds have morphological adaptations that enable attachment to or consumption by animals (Fig. 4a). Similarly, zoochory further increased geographic range size of heavy-seeded species (Fig. 4c). We found a weak correlation between geographic range size and the investigated traits (Fig. 3c), likely due to the role of historical and landscape factors in exotic species' dispersal (e.g. introduction history, suitable habitat availability) (González-Moreno et al. 2014, Pyšek et al. 2015).

We found partial support for the assumption that species able to modify their growth or behavior in response to both environmental context and competition will find it easier to invade a higher diversity of environments (Menzel et al. 2017). In our case study, environmental range size of exotic species was positively related to height variability, but no correlation was found with SLA variability or flexibility in reproductive type (Fig. 3b).

Species with heavier seeds and those with low SLA (slow leaf turnover) reached high local abundance, i.e. dominance (Fig. 4d). Species with these characteristics can be strong competitors with conservative resource use strategies (Amarasekare 2003, Cornwell and Ackerly 2010), and are well-equipped to persist and dominate undisturbed, intact vegetation than plants with high leaf turnover (Reich 2014, Catford et al. 2019). Our dataset was collected from plots of remnant vegetation across the State of Victoria, with a relatively low degree of disturbance.

Our results echo well-known relationships between some demographic processes and functional traits. For example, we provided further evidence that plant height is involved in species' dispersal (Thomson et al. 2011) and height plasticity enables plants to persist under different environmental conditions (Fig. 4). Plant height has been (almost consistently) found to promote species' invasiveness in studies using binary (Gallagher et al. 2015, Moravcová et al. 2015, Divíšek et al. 2018) as well as continuous (Speek et al. 2011) metrics of invasiveness. We also found support for the association of both SLA and seed mass with species' dominance (Fig. 4d). Lower SLA and heavier seed mass each promote plant persistence, especially when environmental conditions are harsh (Grubb 1998, Catford et al. 2019). Seed mass and seed morphology were also found to be involved with species' dispersal (Fig. 4a,c), indicating that the intersection between seed size and dispersal vector is key to understanding dispersal patterns. Previous invasiveness studies that include SLA and seed mass have reported mixed findings, including positive (Dawson et al. 2009, Gallagher et al. 2015, Klinerová et al. 2018), negative

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(Dawson et al. 2009, Moravcová et al. 2015) or non-significant (Gallagher et al. 2015, Divíšek et al. 2018) relationships.

We expected species' ability to reproduce both sexual and asexually would promote multiple demographic dimensions of invasiveness (Table 1) given the previously reported key role of asexual reproduction in invasion (Nunez-Mir et al. 2019). We found that flexibility in reproductive type promoted exotic species' local abundance (Fig. 4d), likely due to species' ability to rely on asexual reproduction while its population size is small, e.g. early invasion. However, reproductive flexibility surprisingly seemed to hamper spread rate and was unrelated to environmental range size (Fig. 3). Finally, our lack of support for the expected role of height in dominance, quantified as local abundance (Fig. 3d), may result from the seasonally dry and nutrient poor environmental conditions characteristic of much of the State of Victoria. In these environments, access to light is not the primary limiting factor, and therefore, being tall does not necessarily correlate with plant persistence (Grubb 1998).

We provide evidence that species' invasiveness encompasses several demographic processes, which have the potential to correlate with a given functional trait in similar, different or even conflicting ways. Our findings also suggest that constellations of multiple traits may be necessary to understand species' performance along different demographic dimensions. For example, heavy seeded plants reached high local abundance (Fig. 4d) but showed slower spread rates when seeds are smooth (Fig. 4a). In another apparent contradiction, we found that species with light and heavy seeds may reach high invasiveness either through quick spread rate (a dimension that is also linked to tall height; Fig. 4a) or dominance (a dimension that also correlates to low SLA; Fig. 4d). Adding to previous research on the context- and stage-dependence of functional traits in invasion (Dawson et al. 2009, Catford et al. 2019), we suggest that focusing on particular demographic mechanisms can further clarify inconsistencies in trait–invasion relationships across different studies. Unfortunately, most functional studies of invasiveness using population-based metrics have focused on the extent of established (or naturalised) species' geographic range, the dimension of invasiveness we found to be most weakly related to functional traits (Fig. 3).

Demographic dynamics and competition with the native community

Attributes of the receiving community (i.e. invasibility; Richardson and Pyšek (2006)), including competition from native plants and the degree of resource fluctuation (Davis et al. 2000),

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influences the relative success of invading species with particular attributes. The demographic metrics we present in this manuscript were estimated for each species as their State-wide ability to become invasive for each demographic dimension. As such, these metrics do not directly represent the species' ability to overcome the local biotic resistance posed by any particular receiving community, neither could they be applied to native communities to represent their ability to inhibit invasions. For example, local abundance, which we interpret as the ability of an exotic plant to become dominant, varies greatly across the diversity of plant communities found in Victoria. It is likely that the traits promoting local abundance of invasive plants, which are assumed to influence native-exotic competition dynamics, will differ across receiving communities with different plant species and traits themselves (McGill et al. 2006). For example, trees with lower SLA and trees with higher wood density exert higher competitive effects on and are less impacted by co-occurring species (Kunstler et al. 2016). Studies of trait effects on competition may provide a better tool to evaluate which invading species may compete strongly with native species.

Limitations and caveats

Our invasiveness models showed low explanatory power (Fig. 3) and, despite their value for understanding how invasion occurs, they may have limited prediction potential. Using a more comprehensive set of traits to evaluate the demographic dimensions of invasiveness may improve model explanatory power. For example, including below-ground traits may provide further insight into invasive species' local abundance. Similarly, metrics of invasiveness that incorporate the local-scale context may improve our ability to use traits to predict species' ability under different scenarios. Our analytical approach required us to overlook the diversity of vegetation formations present across Victoria, including mangroves, temperate rainforests, sub-alpine woodlands and meadows, grasslands, sclerophyll forests, heathlands, semi-arid woodlands and Mallee. Considering local environmental and biotic factors, such as habitat availability and community composition, may be particularly beneficial to further explore trait relationships with geographic range size and local abundance. The demographic dimensions of invasiveness did not explain species' binary invasiveness classifications consistently better than species' traits, except for binary classifications with more restricted ecological criteria (e.g. *Expert opinion limited* and *Semi-quantitative limited*) (Appendix S1: Table S2). This fits with the limited explanation of

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binary invasiveness classifications by traits, particularly those that blend notions of impact with establishing growing populations.

Although “super-invaders”, i.e. species that rank high in multiple invasiveness dimensions, are undoubtedly a priority for management, we decided to approach each dimension independently to simplify inference on the role of traits in particular demographic processes. A focus on individual invasiveness dimensions still presents benefits for the management of particularly damaging invasion outcomes, e.g. invasive species become dominant to the detriment of the indigenous flora and fauna.

Conclusions

Trait-based studies with a clear demography-based approach have the potential to reveal the diversity of ecological strategies that result in successful invasions, enable transparent hypothesis-testing and provided clearer conclusions about the link between traits and invasion than traditional categorical metrics that conflate multiple dimensions (demographic and other types). Concise definitions of invasiveness are also expected to help management decisions because different invasive functional types are expected to have varying degrees of impact (Yokomizo et al. 2009) and likely demand different management actions.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: [link to be added in production]

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DATA AVAILABILITY

Trait records collected by the authors are available in Zenodo (Palma 2020): https://doi.org/10.5281/zenodo.4314008

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Table 1: Variables used in the analyses of the four dimensions of invasiveness, sources and expected effects of traits on dimensions.

Explanatory covariates	**Units/Categories**	**Source***	**Expected trends with invasiveness dimensions****			
			Spread rate	Environmental range size	Geographic range size	Local abundance
Continuous traits						
Height	cm	Field/TRY/BIEN	+		+	+
Seed mass	g	TRY/BIEN	-		-	**V**
SLA	mm^2/mg	Field/TRY/BIEN	+			-
Height variability	standard deviation	Field/TRY/BIEN		+		
SLA variability	standard deviation	Field/TRY/BIEN		+		
Categorical traits						
Longevity	annual^R; perennial	Literature				+
Reproduction type	sexual or asexual^R; both	TRY/Literature/Online	+	+		+
Seed morphology	smooth^R; hooked or fleshy	Literature/Online	+		+	
Wind dispersal	no^R; yes	TRY/Literature		+		
Interactions						
Seed mass * Seed morphology			+		+	
Other						
Minimum residence time	years	AVH			+	
Introduction pathway	accidental^R; deliberate	Government	+			
Management	no^R; yes	Government				-

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^{R}: reference category for analyses. * More details about sources can be found in Appendix S1: Section S3. ** + correlation expected to be positive; **-** correlation expected to be negative; **v** correlation expected to be context-specific. See Introduction for more information.

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Table 2. Six binary classifications: motivation, original categories and number of invasive vs non-invasive species derived from them.

	Source	**Motivation**	**Original categories**	**Invasive taxa**	**Non-invasive taxa**
I Noxious	List of Declared Noxious Weeds in Victoria (http://agriculture.vic.gov.au/).	Highly problematic taxa with economic repercussion. No consideration of ecological attributes	NA	*N=27* Species listed as noxious in Victoria	*N=224* Species not listed as noxious in Victoria
II Literature *	Randall (2007) The introduced flora of Australia and its weed status. CRC for Australia Weed Management, Adelaide.	Collection of different literature references (e.g. lists, reports, ecology-based scientific papers, etc).	'environmental weeds', 'escapees from cultivation', 'agricultural weeds', 'noxious', 'invasive'	*N=50* Species previously reported as 'noxious' or 'invasive' in Australia	*N=201* Species not previously reported as 'noxious' or 'invasive' in Australia
***III Expert opinion inclusive* and**	Re-evaluation of the List of Environmental Weeds of Victoria published by Carr et al. (1992).	Ad-hoc assessment of species based on management potential and ecological criteria. They consider species' biological attributes directly affecting plant demography	'no threat', 'potential threat', 'serious threat', 'very serious threat'	*N=205* Species under 'very serious', 'serious' and 'potential threat' categories	*N=46* Species under remaining categories
IV Expert opinion limited	Re-evaluation of the List of Environmental Weeds of Victoria published by Carr et al. (1992).	Ad-hoc assessment of species based on management potential and ecological criteria. They consider species' biological attributes	'no threat', 'potential threat', 'serious threat', 'very serious threat'	*N=102* Species under 'very serious' and 'serious threat' categories	*N=149* Species under remaining categories

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		directly affecting plant demography			
V Semi-quantitative inclusive	Advisory list of Environmental Weeds in Victoria, developed by the Victorian Department of Environment, Land, Water and Planning (White et al., 2018).	Formal assessment of species based on five attributes: impact on natural ecosystems, area of potential distribution remaining, potential for invasion, rate of dispersal, and range of susceptible habitat types. Management potential is not considered to quantify the risk weeds pose to the environment.	’lower risk’, ’medium risk’, ’moderately high risk’, ’high risk’, ’very high risk’	*N=233* Species declared ’very high’, ’high’, ’moderately high’, or ’medium risk’ weeds	*N=18* Species under remaining categories
VI Semi-quantitative limited	Advisory list of Environmental Weeds in Victoria, developed by the Victorian Department of Environment, Land, Water and Planning (White et al., 2018).	Formal assessment of species based on five attributes: impact on natural ecosystems, area of potential distribution remaining, potential for invasion, rate of dispersal, and range of susceptible habitat types. Management potential is not considered to	’lower risk’, ’medium risk’, ’moderately high risk’, ’high risk’, ’very high risk’	*N=88* Species declared ’very high’ or ’high risk’ weeds	*N=163* Species under remaining categories

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quantify the risk weeds
pose to the environment.

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* We based our binary categorization on the original 'noxious' and 'invasive' categories. All the species in this study have been described as 'environmental weeds', 'escapee from cultivation' and 'agricultural weed' at least once in Australia, preventing inference based on these descriptors.

Figure 1. Hypothesized relationships between demographic dimensions of invasiveness and functional traits (Table 1). Positive correlations between the trait and the dimension in green; negative correlation in purple. Black means the correlation is context dependent.

Figure 2. Predicted effect of traits and minimum residence time on ten invasiveness metrics. Effects on (a) the probability of being classified as an invasive plant under the *I – Noxious* (R^2=0.16), *II - Literature* (R^2=0.21), *III - Expert Opinion inclusive* (R^2=0.07), *IV - Expert Opinion limited* (R^2=0.11), *V - Semi-quantitative inclusive* (R^2=0.16) and *VI - Semi-quantitative limited* (R^2=0.04) binary classifications, and (b) the continuous dimensions of invasiveness (Spread rate, R^2=0.06; Environmental range size, R^2=0.12; Geographic range size, R^2=0.10; and Local abundance, R^2=0.04). Model covariate structure was identical for all responses (n=251); all five covariates were included in each. Dots represent average effects and lines represent 95% credible intervals. Positive effects in red; negative effects in blue; non-significant effects in black.

Figure 3. Predicted effect of traits and other covariates on (a) spread rate (n=236, R^2=0.03), (b) environmental range size (n=228, R^2=0.08), (c) geographic range size (n=299, R^2=0.06) and (d) local abundance (n=236, R^2<0.01). Dots represent average effects and lines represent 95%

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credible intervals. Positive effects in red; negative effects in blue; non-significant effects in black. Areas of the plots where correlations were expected (Table 1) shaded in grey. Plots show effect of perennial longevity, sexual and asexual reproduction, hooked/fleshy seeds and wind dispersal compared to annual/biennial longevity, sexual or asexual reproduction, smooth seeds and other dispersal vectors, respectively. Note the narrow credible intervals for the effect of wind dispersal (panel c).

Figure 4. Predicted maximum spread rate (a), environmental range size (b), geographic range size (c) and local abundance (d) of exotic plants across values or categories of traits. Black dots and lines represent the estimated average response and grey shade represents the estimated 95% credible intervals. Grey dots represent the mean trait values of the species included in the analyses. Figure only shows relationships that are statistically significant from analyses in *Question 2: Traits and demographic dimensions of invasiveness*, with the exception of SLA and local abundance (panel d).

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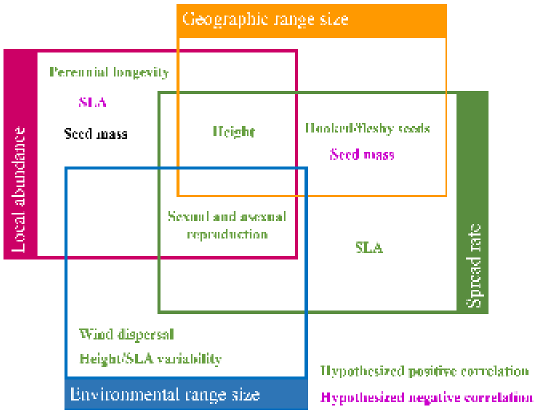

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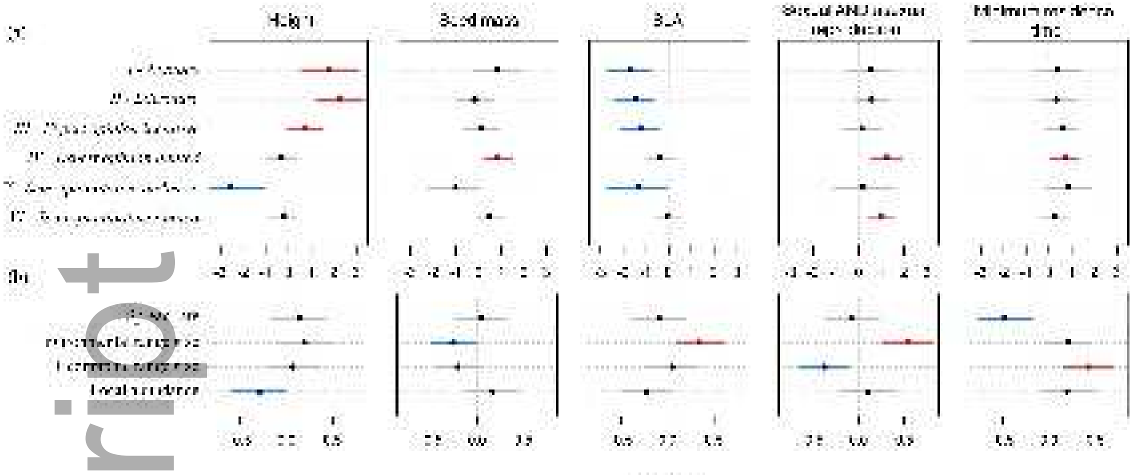

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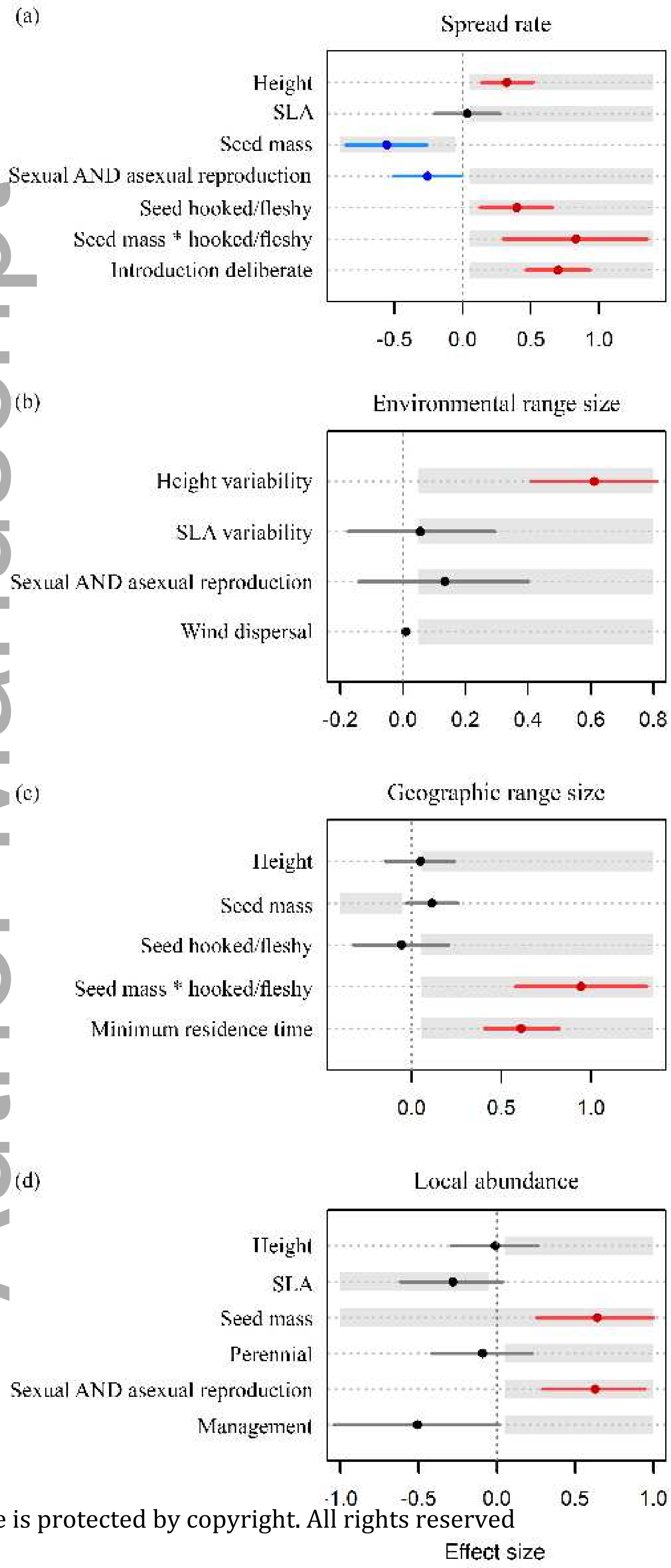

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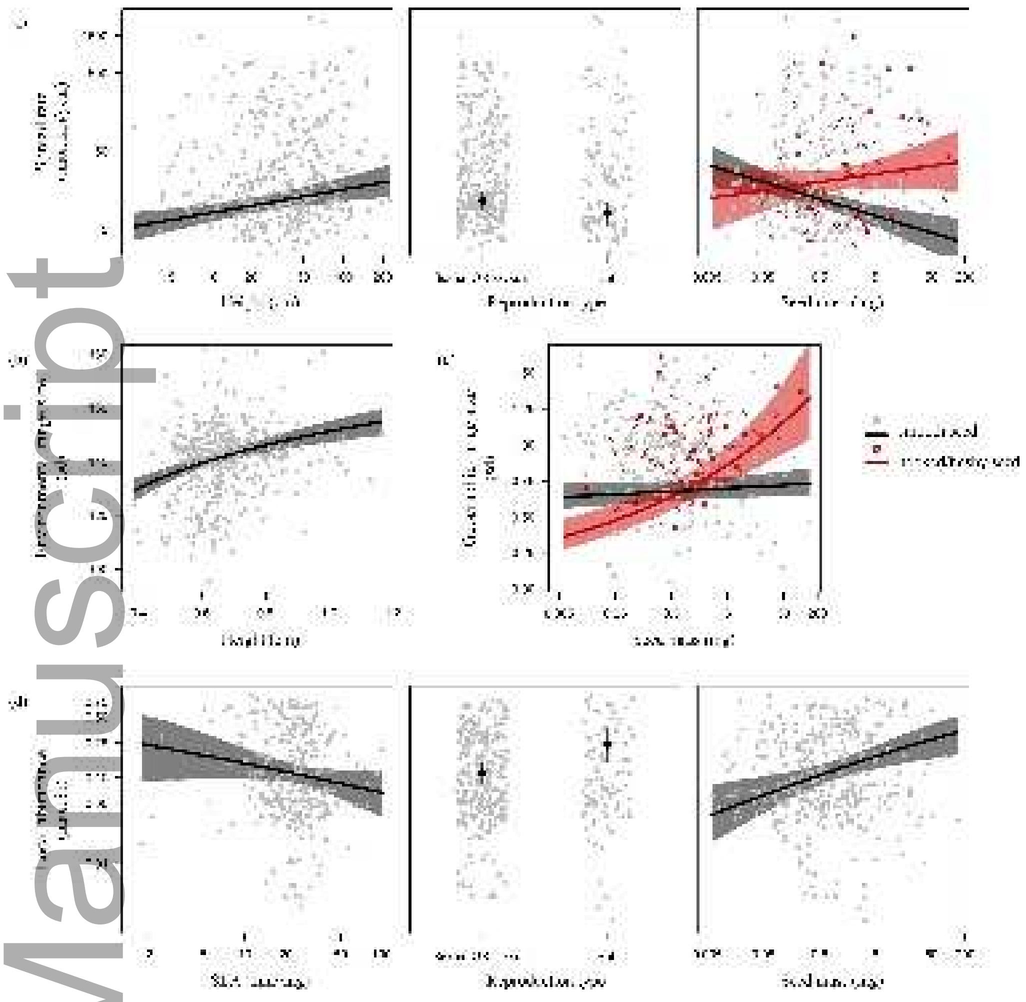

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