The Comparative Demography of Invasive Plants

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I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

(Signature) ………………………………………………………………………………

Abstract

Biodiversity, ecosystems, industry and human health are threatened by invasive plant species. The costs of mitigating damages run into billions of pounds per annum. Fundamental to the control of invasive plant species is an ability to predict which species will become invasive. Yet identification of predictive differences between invasive and non-invasive species has proven difficult to pinpoint. In this thesis I identify several weaknesses within published literature, and using field experiments and meta-analyses we address these to find consistent predictors of invasiveness amongst plants. Specifically, I recognize that predictors of invasiveness can be identified by studying plant species in the native range because species may undergo phenotypic and demographic changes following naturalization (Chapters 2 – 5). I also recognize the importance of comparing globally invasive and non-invasive species, and the importance of accounting for phylogenetic relationships so as not to inflate or conceal differences (Chapters 2 – 4). Finally, I investigate whether particular analyses are more appropriate for investigating life history and demographic differences (Chapter 5).

This thesis comprises an introductory chapter (Chapter 1), four data chapters (Chapters 2 - 5) and a general discussion (Chapter 6). Chapters 2 and 3 compare life history traits of plant species known to be invasive elsewhere, with their exported but non-invasive sympatric relatives in the native range. Chapter 4 utilizes Population Projection Matrices held within the COMPADRE Plant Matrix Database, to compare demographic projections of stable and transient dynamics of invasive and non-invasive plants; and Chapter 5 compares ten metrics, derived from Population Projection Matrices, of seven invasive species between the native and invaded range to determine if there are demographic or life history differences that facilitate invasion, and to identify those analyses that are most likely to reveal such differences.

I find reproductive capacity to be a predictor of invasiveness, and that analyses of transient dynamics are more likely than analyses of projected stable dynamics to reveal demographic or life history differences between invasive and non-invasive species or populations of plants. I

discuss these findings in the context of invasive risk assessment protocols and highlight future research opportunities.

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Chapter 1

Introduction

Invasive Species

Invasive species, variously defined as those species that are transported outside of their native range, and which establish and spread to cause ecological, environmental and economic harm (Daehler, 2003, IUCN, 1999, Beck et al., 2008), rank among the major threats to global biodiversity (Butchart et al., 2010, Wilcove et al., 1998, Hooper et al., 2012, Clavero and García-Berthou, 2005). Impacts can be described in terms of socio-cultural and economic harm (Bradley et al., 2006, Pimentel et al., 2005), or environmental harm encompassing reduced fitness and extinction of native species, and ecosystem degradation (Vila et al., 2011, Hejda et al., 2009, Clavero and García-Berthou, 2005, Hooper et al., 2012). There are many examples of invasive species outcompeting native species, and of biotic and genetic homogenization, whereby invasive species weaken the uniqueness of distinct biotas and species following hybridization (Olden, 2006, Ryan et al., 2009, Winter et al., 2009). Individually or in combination, these impacts have potential to alter ecosystem processes and de-value ecosystem services (Ehrenfeld, 2010, Vila et al., 2011). Invasive plant species alone cost the global economy in excess of £300 billion per year to manage invasive populations for the purpose of curtailing impacts on biodiversity, ecosystem services, production and construction projects, and for losses incurred as a result of reduced yield, recreational activity, erosion, fire and water retention (Williams, 2010). Consequently, identifying traits of invasive plant species and the mechanisms linked with invasion success has been a key objective for invasion biologists and ecologists alike (Burns et al., 2013, Hovick et al., 2012, Castro-Díez et al., 2011, Davidson et al., 2011, Prentis et al., 2008, Agrawal et al., 2005). Yet there exist numerous definitions of what constitutes an ‘invasive species’ (Pysek et al., 2004; Richardson et al., 2000). Blackburn et al. (2011) recognized that the inconsistent use of definitions in scientific studies has potential to hamper invasive species research, and in response, developed the unified framework for biological invasions. This framework comprises four stages: transportation, introduction, establishment and spread. In this thesis, an invasive plant species is defined as a species that has both established and spread to cause ecological, environmental and/ or economic harm. This definition falls into the fourth stage of Blackburn's et al. (2011) unified framework for biological invasion.

Traits of Invasive Plant Species and Research Methods

To date, attempts to understand and/or predict invasion success of plants have variously used functional trait analyses (Goodwin et al., 1999, Rejmánek and Richardson, 1996, Burns, 2006), demographic analyses (Burns et al., 2013, Jongejans et al., 2008, Ramula et al., 2008, Buckley et al., 2010), spread rate models (Hastings et al., 2006), and ecosystem invasibility approaches (Catford et al., 2011, Küehn and Klotz, 2007). These approaches have revealed that some environments are more susceptible to invasion (D'Antonio et al., 1999, Marvier et al., 2004), and are more likely to be invaded by a particular plant life-form (Pyšek and Prach, 1995, Williamson and Fitter, 1996, Dukes, 2001). Correlates of invasiveness include, in some instances, a history of invasiveness elsewhere, native latitudinal range, propagule pressure, time since introduction and plant attractiveness (Goodwin et al., 1999, Reichard and Hamilton, 1997, Herron et al., 2007, Richardson and Pyšek, 2006). Invasive plant species typically exhibit clonal reproduction (Song et al., 2013), or autonomous seed production (Hao et al., 2011), and in comparison to rare plants are more likely to be polyploid as opposed to diploid (Pandit et al., 2011). Relative to native, or to introduced but non-invasive plant species, invasive species can be taller (Pyšek and Richardson, 2007, Reichard and Hamilton, 1997, Crawley et al., 1996), have a greater biomass (Schlaepfer et al., 2010), shorter generation time (Grotkopp et al., 2002), faster and more profuse germination (van Kleunen and Johnson, 2007), longer fruiting period (Reichard, 1994, Cadotte and Lovett-Doust, 2001), higher relative growth rate and a larger specific leaf area (Rejmánek and Richardson, 1996, Burns, 2006), higher fecundity (Burns et al., 2013, Moravcová et al., 2010, Mason et al., 2008, Burns, 2006), smaller seed mass (Hamilton et al., 2005, Grotkopp et al., 2002) (Rejmánek and Richardson, 1996), and in some instances larger seed mass (Daws et al., 2007). Given the array of identified correlates, it is perhaps not surprising that few have been consistently associated with invasiveness (Pyšek and Richardson, 2007).

As a consequence, weed risk assessment protocols assess the likelihood of a species becoming 'invasive' on a combination of these correlates (Pheloung, 2001, Gordon et al., 2008, Groves et al., 2001, Hulme, 2012). Despite this conservative approach our ability to predict which species become invasive remains weak at best. A fundamental goal of invasive species research must therefore be to identify key traits that predispose species to becoming invasive outside their native range.

Knowledge Gaps in Invasive Species Research

This thesis identifies a number of weaknesses in the experimental framework used to predict plant invasiveness to date, and subsequently addresses several unexplored questions in the ecology of invasive species. Before the novelty of this thesis is discussed, the key literature that lead to our observations and hypotheses is summarized as follows:

Baker (1965) postulated that invasive plant species will possess a number of traits such as large size, high fecundity and rapid growth, which convey an advantage over co-occurring, non-invasive species. To date, invasive plant species have been shown to a) be larger than the native or non-invasive introduced species (Pyšek and Richardson, 2007, Reichard and Hamilton, 1997, Crawley et al., 1996, van KleunenWeber et al., 2010); b) grow faster than their non-invasive relatives in the invaded range (Rejmánek and Richardson, 1996, Burns, 2006); and c) grow faster and achieve a larger size (biomass, root: shoot ratio and leaf length) than their non-invasive congeners in the native range (van Kleunen et al., 2011, Tolvanen et al., 2001). Large size however, has not been consistently associated with invasiveness (Burns, 2006).

In the invaded range high fecundity (seed production) and propagule pressure (the number of dispersal units reaching a new site) are correlates of invasiveness (Burns et al., 2013, Burns, 2006, Moravcová et al., 2010, Mason et al., 2008, Reichard and Hamilton, 1997, Grotkopp et al., 2002, Herron et al., 2007). It is intuitive that more fecund individuals or species have greater opportunity to colonize new sites due to the greater number of dispersal units generated (Westoby et al., 2002). However, evidence for this is inconsistent (Daehler, 2003) and surprisingly scarce. I attribute this to the scarcity of fecundity data, which can be time consuming to measure and when collected for the purpose of modelling population demographics, is typically not presented in the source literature.

A conundrum is posed by small seed mass, a correlate of increased fecundity (Mason et al., 2008, Muller-Landau, 2010, Turnbull et al., 1999) but not a consistent correlate of invasiveness (Schlaepfer et al., 2010, van Kleunen and Johnson, 2007, Dawson et al., 2011, Mihulka et al., 2003). Small seed mass has been identified as a correlate of invasiveness in some instances (Hamilton et al., 2005, Grotkopp et al., 2002, Rejmánek and Richardson, 1996, Graebner et al., 2012) but not in others (Schlaepfer et al., 2010, van Kleunen and Johnson, 2007, Dawson et al., 2011, Mihulka et al., 2003). Furthermore, the reverse can be true: invasive species have been shown to exhibit larger seed mass than a) their co-occurring native relatives (Daws et al., 2007); and b) introduced non-invasive species (Lake and Leishman, 2004) in the introduced range. This irregularity is interesting because smaller-seeded species are typically more fecund than larger-seeded species (Turnbull et al., 1999, Rees and Westoby, 1997, Coomes and Grubb, 2003), and because high fecundity is a frequently cited correlate of invasiveness in the invaded range (Burns et al., 2013, Burns, 2006, Moravcová et al., 2010, Mason et al., 2008). Invasive species should therefore exhibit consistently smaller seed mass than non-invasive species, but this is not the case (Schlaepfer et al., 2010, van Kleunen and Johnson, 2007, Dawson et al., 2011, Mihulka et al., 2003). Theory proposes that seed mass (and by extension fecundity) is controlled by a trade-off either between competition and colonization (Turnbull et al., 1999), or between fecundity and tolerance of stressors (Muller-Landau, 2010). These theories explain how species with larger seeds generate larger and stronger seedlings, which are competitively superior or exhibit greater tolerance to adverse conditions but consequently trade off seed mass against seed number. There is good evidence that larger seeds produce larger seedlings (Turnbull et al., 1999, Herrera and Laterra, 2009), and that in some instances seed mass increases between the native and invaded range (Hierro et al., 2013, Graebner et al., 2012, Buckley et al., 2003). This indicates that larger seeds are beneficial; yet high fecundity and propagule pressure, both identified correlates of invasiveness in the invaded range, trade off against large seed mass. The literature does not address the observed seed mass - fecundity paradox within the context of invasive plants.

The trait-based approaches discussed above, whilst extremely valuable, have important weaknesses that limit their suitability for identifying predictors of invasiveness. Because these weaknesses also apply to demographic studies, I reserve further discussion until after the findings and implications of demographic studies are fully explored.

Thus far Chapter 1 focuses on individual phenotypic and demographic traits associated with invasiveness rather than the effect that such traits have on population performance. Demography, the study of parameters such as birth, mortality and fecundity that determine population size and structure through time (Harper and White, 1974), encompasses the effect of phenotypic and demographic traits, and environment, on population performance or spread rate, a proxy of invasiveness. Population Projection Matrices (PPM) split life cycles into life-stages, and contain life history information as rates of transition or vital rates (stage-specific recruitment, stasis & progression) (Stott et al., 2010), and as demographic properties such as the stable population growth rate, and indices of transient dynamics (e.g. population inertia (ρ_∞) and reactivity) (Caswell, 2001). Demographic analyses can therefore be used to explore multiple approaches in unison. Such analyses have been widely used to inform invasive species management strategies (DeWalt, 2006, Emery and Gross, 2005, Golubov et al., 1999, Hastings et al., 2006, Emery et al., 1999, Evans et al., 2012) but demographic meta-analyses and multi-species approaches are few (*c.f.* Ramula et al. (2008), Burns et al. (2013), Iles et al. (2016)) and provide a potentially powerful tool for predicting invasiveness. Those studies that have been undertaken have shown that invasive populations tend to exhibit higher projected population growth than 1) native populations (Ramula et al., 2008), and 2) introduced populations of non-invasive congeners with which they co-occur (Burns et al., 2013). These studies also revealed fecundity (Burns et al., 2013) and growth (Ramula et al., 2008) to be of greater importance for invasive species than native or non-invasive introduced species, and amongst conspecific native populations (Parker et al., 2013). Also of relevance is the observation that highly fecund species have a superior ability to amplify or boom in response to exogenous disturbances (Stott et al., 2010), and amongst introduced species, exhibit more favourable transient dynamics (short-term population dynamics), greater long-term population growth and increased population viability (proxies of invasiveness) (Iles et al., 2016). Such findings potentially provide the beginnings of a framework for identifying the invasive species of the future. However, the demographic and trait-based approaches discussed above suffer a number of weaknesses that limit their suitability for identifying predictors of invasiveness. These are listed below:

1) All but a few studies (Schlaepfer et al., 2010, van Kleunen et al., 2011, van Kleunen and Johnson, 2007) are performed in the invaded range. This approach potentially conflates invasiveness predictors with changes that occur during invasion. For example, it has been illustrated that seed size (Hierro et al., 2013, Graebner et al., 2012, Buckley et al., 2003) and fecundity (Parker et al., 2013) can increase between the native and invaded range, and that the environment contributes to variation in demographic parameters and predictions (Buckley et al., 2010, Morris and Doak, 2005, Nantel et al., 1996). Measurement of demographic parameters and phenotypic traits in the invaded range might therefore measure changes caused by the new environment. Under this scenario, identified correlates explain rather than predict invasiveness. It can be reasoned that invasive risk assessments protocols informed with explanations of invasiveness are not necessarily well suited to identify predictors of invasiveness and prevent further introductions of species that subsequently become invasive. This highlights the importance of selecting a study system (i.e. native, invaded or introduced range) appropriate to the research question (van Kleunen et al., 2010). Of the few studies performed in the native range (Schlaepfer et al., 2010, van Kleunen et al., 2011, van Kleunen and Johnson, 2007) none consider demographic traits as potential correlates of invasiveness.

2) Previous studies compare invasive species with species that are native or non-invasive at the location of study, but that are reported to be invasive elsewhere (*c.f.* van Kleunen et al., 2010).

Under this scenario, an "invasiveness" trait or syndrome could be obscured or weakened by comparisons with species that are in fact invasive elsewhere.

3) Previous studies (Burns et al., 2013, Burns, 2006, Moravcová et al., 2010, Mason et al., 2008) did not consider the effect of plant size on fecundity. Plant size is important because larger individuals ordinarily exhibit higher fecundity (Weiner et al., 2009) and because greater plant biomass (Schlaepfer et al., 2010, van Kleunen et al., 2011), height and larger specific leaf area (Rejmánek and Richardson, 1996, Pyšek and Richardson, 2007) have been identified as correlates of invasiveness. In the absence of considering plant size, previous studies were unable to determine if invasive plant species exhibit a constitutively higher fecundity (higher fecundity per-unit-size) or are larger and are therefore more fecund than non-invasive species.

4) None recognise the seed mass: fecundity paradox. If fecundity in the native range were an important predictor of invasiveness as suggested by studies in the invaded range, invasive species would be expected to exhibit a significantly smaller seed mass than their sympatric non-invasive congeners. Alternatively, it would be predicted that invasive species are those which escape the typical trade-offs of competition and colonization, or of fecundity and tolerance, and therefore exhibit higher fecundity than non-invasive species, without a corresponding reduction in seed mass.

5) Whilst several studies account for the effect of phylogeny using congeneric pairs (Burns et al., 2013, Schlaepfer et al., 2010, van Kleunen et al., 2011), none explore the potential of phylogeny to predict invasiveness. Such opportunities have been hampered in the absence of demographic data for a large number of species that are representative of a diversity of plant families.

Scope of Thesis

This thesis addresses the shortcomings and explores the research opportunities listed above by studying life history traits of invasive and non-invasive plants in 1) the native range, in order to predict rather than explain, invasiveness; and 2) between ranges to identify changes in demographic performance that facilitate invasion success, whilst simultaneously controlling for phylogeny, environment and global invasive status. This work has resulted in four discrete data chapters (Chapters 2 – 5), which collectively provide new insights into the ecology of invasive species. Chapter 2 focuses on wild plants in their native range to compare life history traits of species known to be invasive elsewhere, with their exported but non-invasive sympatric relatives. Specifically, Chapter 2 compares plant size between invasives and non-invasives, then controls for plant size to ask whether invasive plants exhibit higher fecundity, and higher probability of seed-set, than non-invasives. Using the same wild populations Chapter 3 asks whether invasive and non-invasive congeners differ in seed mass, reproductive investment (seed production x seed mass) and germination probability. Chapter 3 builds on the findings of Chapter 2 by addressing the unexplored seed mass – fecundity paradox in the ecology of invasive plant species. Chapter 4, a meta-analysis utilizing 1202 spatial populations representing 501 plant species from the COMPADRE Plant Matrix Database (COMPADRE 3.0.0) (Salguero-Gómez et al., 2014), compares the stable rate of population increase (λ_{max}) and inertia (ρ_∞) [a measure of how much larger or smaller a non-stable population becomes compared with an equivalent stable population, as a result of transient dynamics (Stott et al., 2012)] of invasive and non-invasive plants, whilst simultaneously controlling for phylogeny, range [native or naturalised] and global invasion status. Chapter 5 builds on Chapter 4 by comparing the demographic performance of seven invasive species between the native and invaded range to determine if demographic processes change between ranges, and also to identify the type of analyses that are most likely to reveal demographic or life history differences that facilitate invasion.

Finally, the discussion draws together the findings of each chapter and presents a framework for identifying those plant species to be quarantined in order to prevent further deleterious introductions and establishment of invasive populations. The consequences for existing weed risk assessment protocols are discussed, and future research opportunities highlighted.

Thesis Format and Structure

Chapters 2 – 5 are presented in their published or submitted form. Each chapter is therefore presented in a different format in accordance with the journal specific submission guidelines. There may be some repetition between chapters, particularly within method sections due to overlapping methodologies. In accordance with submission guidelines, references are presented after each chapter.

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Chapter 2:

Jelbert, K., Stott, I., McDonald, R. A. & Hodgson, D. Invasiveness of plants is predicted by size and fecundity in the native range. *Ecology and Evolution* **5**, 1933-1943, (2015).

Invasiveness of plants is predicted by size and fecundity in the native range

Abstract

1. An important goal for invasive species research is to find key traits of species that predispose them to being invasive outside their native range.
2. Comparative studies have revealed phenotypic and demographic traits that correlate with invasiveness among plants. However, all but a few previous studies have been performed in the invaded range, an approach which potentially conflates predictors of invasiveness with changes that happen during the invasion process itself.
3. Here we focus on wild plants in their native range to compare life history traits of species known to be invasive elsewhere, with their exported but non-invasive relatives. Specifically we test four hypotheses: that invasive plant species 1) are larger; 2) are more fecund; 3) exhibit higher fecundity for a given size; and 4) attempt to make seed more frequently, than their non-invasive relatives in the native range. We control for the effects of environment and phylogeny by using sympatric congeneric or confamilial pairs in the native range.
4. We find that invasive species are larger than non-invasive relatives. Greater size yields greater fecundity, but we also find that invasives are more fecund per-unit-size.
5. Synthesis: We provide the first multi-species, taxonomically controlled comparison of size and fecundity of invasive versus non-invasive plants in their native range. We find that invasive species are bigger, and produce more seeds, even when we account for their differences in size. Our findings demonstrate that invasive plant species are likely to be invasive as a result of both greater size and constitutively higher fecundity. This suggests that size and fecundity, relative to related species, could be used to predict which plants should be quarantined.

Keywords: basal stem diameter, demography, fecundity, invasive, native, phylogeny, plant

Introduction

Invasive species consistently rank among the five major threats to biodiversity, worldwide (Sala *et al.* 2000; Butchart *et al.* 2010; Kareiva & Marvier 2011) and are costly to the global economy (Pimentel, Zuniga & Morrison 2005). Given the economic (Pimentel, Zuniga & Morrison 2005) and ecological costs of invasive plant species (Vilà *et al.* 2011), it is unsurprising that considerable attention has been given to understanding the characteristics (Rejmánek & Richardson 1996; Ramula *et al.* 2008; Pyšek, Křivánek & Jarošík 2009; Burns *et al.* 2013) and the underlying mechanisms associated with invasion success (Prentis *et al.* 2008; Davidson, Jennions & Nicotra 2011). The many traits and mechanisms thought to influence invasiveness have been reviewed extensively elsewhere (Pyšek & Richardson 2007; Prentis *et al.* 2008; van Kleunen, Weber & Fischer 2010; Davidson, Jennions & Nicotra 2011); here we focus on the demographic traits of size and fecundity, first because they provide a close link between phenotype, life history and population dynamics (Stott, Townley & Hodgson 2011) and second because, if shown to be markers of invasiveness, they are relatively simple to measure in the field.

As postulated by Baker (1965), it is intuitive that invasive species will be more fecund and grow faster than non-invasive species. Fast growth and large size may afford introduced species an advantage over the floristic assemblage of the invaded environment. Evidence for this comes from studies that have shown invasive species to a) be larger than their native or non-invasive introduced counterparts (Reichard & Hamilton 1997; Pyšek & Richardson 2007; van Kleunen, Weber & Fischer 2010); b) grow faster than their non-invasive congeners in the invaded range (Grotkopp, Rejmánek & Rost 2002; Burns 2006); and c) grow faster and attain a larger size (biomass, root: shoot ratio and leaf length) than their non-invasive congeners in the native range (van Kleunen *et al.* 2011). However, Burns (2006) found that invasive species of Commelinaceae were not significantly larger than their non-invasive congeners. Fecundity has also been identified as an important correlate of invasiveness in the invaded range (Burns 2006; Mason *et al.* 2008; Moravcová *et al.* 2010; Burns *et al.* 2013). Propagule pressure (the number of seeds or viable clonal material reaching a new site) is an important correlate of invasiveness

(Holle & Simberloff 2005), therefore more fecund individuals or species can be assumed to have greater opportunity to colonize new sites (Westoby *et al.* 2002). However, evidence for this is both conflicting and surprisingly scarce. We attribute this to the paucity of fecundity data in field guides, which form a typical source of data for comparative analyses of traits associated with invasiveness. In the invaded range, invasive species have been shown to exhibit higher fecundity than a) their introduced, non-invasive congeners (Burns 2006; Burns *et al.* 2013), b) non-invasive, introduced, unrelated species (Moravcová *et al.* 2010), and c) native species (Mason *et al.* 2008). However, conversely, Daehler (2003) found that of thirteen comparisons of invasive-native confamilial pairings in the invaded range, invasive species had no consistent reproductive advantage over co-occurring natives.

These approaches, whilst enormously valuable, have three weaknesses that limit their suitability for identifying predictors of invasiveness:

1) All, with the exception of (van Kleunen & Johnson 2007; Schlaepfer *et al.* 2010; van Kleunen *et al.* 2011), are performed in the invaded range, an approach which conflates predictors of invasiveness with changes that may happen during the invasion process. Of the studies performed in the native range (van Kleunen & Johnson 2007; Schlaepfer *et al.* 2010; van Kleunen *et al.* 2011), none consider fecundity as a potential correlate of invasiveness. Environmental variation is known to contribute to significant variation in demographic parameters and predictions (Morris & Doak 2005; Buckley *et al.* 2010). Measuring demographic parameters, such as fecundity, in the invaded range, is therefore a measure following change induced by the novel environment. We suggest that demographic parameters associated with invasiveness in the invaded range may be poor predictors of invasiveness, when the objective is to identify potential invaders prior to their introduction.

2) All but one study (van Kleunen, Weber & Fischer 2010) compare invasive species with species that are native or non-invasive at the study location only: several of these native or 'non-invasive' species are known to be invasive elsewhere. If invasive species share an

"invasiveness" trait or syndrome, we should expect comparisons with species that are invasive elsewhere to mask or weaken potential correlates of invasiveness.

3) None considers the effect of plant size on fecundity. Plant size is critical because we know that within a species, larger individuals typically exhibit higher fecundity (Weiner *et al.* 2009) and because increased plant height, larger specific leaf area (Grotkopp, Rejmánek & Rost 2002; Pyšek & Richardson 2007) and biomass (Schlaepfer *et al.* 2010; van Kleunen *et al.* 2011) have been identified as correlates of invasiveness. This raises an important question: are invasive plant species invasive because they are larger and therefore more fecund, or because they exhibit a constitutively higher fecundity, i.e. higher fecundity per-unit-size, than their non-invasive counterparts?

Here we focus on traits expressed by wild plants in their native range, and compare them between species that are invasive elsewhere, and species that are established elsewhere but not invasive. We control for the effects of phylogeny by using congener/ confamilial pairs (Burns *et al.* 2013). We also control for environmental effects by studying sympatric populations in a restricted geographical zone (mid and west Cornwall, UK). We hypothesize that invasive plants 1) are larger than their native, non-invasive relatives; 2) are therefore more fecund; 3) but for a given size, exhibit higher fecundity; and 4) attempt to make seed more frequently than their native, non-invasive relatives. To our knowledge, this is the first study to investigate fecundity in the native range as a predictor of invasiveness. This novel approach accounts for the potential effects of phylogeny, environment and global invasive status, and has the potential to identify true differences in life history parameters (in this instance size and fecundity) between invasive and non-invasive species.

Materials and Methods

Species

Five sympatric congener/ confamilial pairs of plant species (Table 1) were selected on the basis that each pair a) comprised one native species that is invasive elsewhere and one native species that is introduced but non-invasive elsewhere, b) occurred sympatrically in the native range, c) comprised accessible and sufficiently large populations to facilitate monitoring, and d) represented a broad range of angiosperm families. Where possible, species pairs e) occupied a similar geographical native range, and f) belonged to the same life-form (i.e. perennial or annual; herb or shrub).

Plant status was determined by searching the Global Invasive Species Database (GISD) http://www.issg.org/database, the Invasive Species Compendium (CABI) http://www.cabi.org/isc, the Australian Invasive Weed List http://www.environment.gov.au/biodiversity/invasive/weeds/index.html, the Australian Plant Census (CHAH) http://biodiversity.org.au/apni.reference/181584, the European and Mediterranean Plant Protection Organization (EPPO) database http://www.eppo.int/DATABASES/databases.htm, Schedule 9 of the Wildlife and Countryside Act (1981) http://jncc.defra.gov.uk, the United States Department of Agriculture (USDA) Plant Database http://plants.usda.gov/checklist.html, the National Institute for Environmental Studies (NIES) invasive species of Japan database http://www.nies.go.jp/biodiversity/invasive, the National Pest Plant Accord http://www.mpi.govt.nz and by using the following search term in Google '*Latin name* invasive' (accessed April 2013). Species are considered invasive when designated as 'invasive' (also 'weedy' or 'noxious' in the USDA Plant Database) in one or more of the databases listed above or when designated as invasive by a Government Agency or Academic Institution. CABI cites two of our 'invasive' congeners (*Silene dioica* and *Rhinanthus minor subsp. minor*) as invasive. Whilst this status could not be verified from the CABI cited literature, both species are notoriously 'weedy' (Hulst, Shipley & Thériault 1987; Jenkins & Keller 2011), and have more citations in the Global Compendium of Weeds (GCWs) than their 'non-invasive' congeners (Randall 2012). The GCWs collates citations referring to 'weedy behavior' outside of the native range; the number of citations for each listed species has been used previously to determine global invasive status, and to successively identify correlates of invasiveness (Schlaepfer *et al.* 2010; Jenkins & Keller 2011). We therefore consider the designation of these species as 'invasive' to be correct. A species was considered to be ‘introduced’ if it was naturalised outside of its native range. A species was considered to be native to the UK if listed as such on the Online Atlas of the British and Irish Flora http://www.brc.ac.uk/plantatlas/.

Table 1. Species pairs: life form, breeding system, status and mean seed production per inflorescence

Family	**Species**	**Common Name**	**Life-Form**	**Breeding System***	**Mean Seed Production Per Inflorescence**	**Status**	**Citation**
Caryophyllaceae	*Cerastium fontanum*	Common mouse-ear	Per	Hermaphrodite; protoandrous; automatic self or cross	52	Invasive	USDA; ISSG
	Cerastium diffusum	Sea mouse-ear	Ann	Hermaphrodite; automatic self	19	Introduced	USDA
Caryophyllaceae	*Silene dioica*	Red campion	Per	Dioecious; obligatory cross	277	Invasive	(Jenkins & Keller 2011); CABI; (Randall 2012)**
	Silene uniflora	Sea campion	Per	Gynodioecious; protoandrous; automatic self or cross	57	Introduced	CHAH
Ericaceae	*Calluna vulgaris*	Heather	Shrub	Hermaphrodite; weakly protoandrous; cross	8	Invasive	Australian Invasive Weed List; National Pest Plant Accord; ISSG
	Erica cinerea	Bell heather	Shrub	Hermaphrodite; weakly protoandrous; cross or automatic self	16	Introduced	CHAH
Scrophulariaceae	*Rhinanthus minor* subsp. *Minor*	Yellow rattle	Ann	Hermaphrodite; automatic self or cross	11	Invasive	(Hulst, Shipley & Thériault 1987); CABI; (Randall 2012)**
	Pedicularis sylvatica	Lousewort	Per	Hermaphrodite; cross	13	Introduced	USDA
Apiaceae	*Daucus carota*	Wild carrot	Per	Hermaphrodite; protoandrous; cross	934	Invasive	USDA
	Eryngium maritimum	Sea holly	Per	Hermaphrodite; protoandrous; cross	44	Introduced	USDA

* Mating system derived from http://www.ecoflora.co.uk

** Invasive status based on number of citations in the GCWs (Randall 2012)

Location

Each study location (five in total: one for each species pair) was selected on the bases that it supported both species of each sympatric pair, and that these populations could reliably be assumed to be native. To ensure that the sample populations were of native provenance, all sites were characterized by natural or semi-natural vegetation, and sites were excluded where past and present management had the potential to have introduced plants of unknown provenance. Sites supporting sympatric species pairs were identified using the ERICA Database held by Dr. Colin French. ERICA, a database compiled by amateur and professional botanists, holds more than 1.3 million geo-referenced vascular plant records of the Cornish flora. To locate our sample populations we produced co-incidence maps showing the 100m distribution of each congener pair. Accessible sites were then ground-truthed to locate each sympatric population.

Data Collection

Permanently marked, geo-referenced quadrats were installed at each site. These were positioned in order to capture a representative sample of each sympatric population. Quadrat size was determined by the species' area-weighted density and ranged from 0.5 x 0.5m to 1m x 1m. Larger species typically necessitated larger quadrats; however, within each species pair, quadrat size was the same. The number of quadrats sited per species ranged from eight to thirteen (mean = 10); this variation is a result of the species area-weighted density and abundance at the site. Each quadrat (permanently marked with buried metal chips) was made relocatable using a Global Positioning System (GPS) to provide a coarse location (accurate to within 10m), and a metal detector to determine the exact location.

Individual plants within each quadrat were marked with coloured, biodegradable, hemp string and were assigned a unique identification number corresponding to the individual's position within the quadrat. We consider an individual to be an entire plant or, for clonal rhizomatous species, a ramet (an individual belonging to a clonal group of genetically identical individuals) and use the term 'plant(s)' interchangeably to refer to these individuals in this paper. Using the physical markers and/or the unique identification code it was possible to locate the same individuals repeatedly between May and November 2013, encompassing late spring, summer and autumn. Each sample population was relocated on three occasions, the timing of which was determined by the reported plant life cycle and by interim visits. During each visit, we measured plant size (basal stem diameter, rosette diameter and rosette perpendicular diameter) and recorded the life-stage (i.e. seedling, vegetative, reproductive etc.) of all individuals within each quadrat. Basal stem diameter, defined as the diameter of the stem at ground level, was carefully measured to avoid damaging the plant, using 150mm, 0.1mm precision, dialMax Vernier Dial Calipers. If present, we also recorded the number of seed capsules or racemes per plant (from which we calculated fecundity as described below). *Silene dioica* and to a lesser extent *Cerastium fontanum* were observed to exhibit a long flowering period lasting, in some instances, the duration of our study. For these species the reported fecundity measure is considered conservative. Fortunately both *Silene dioica* and *Cerastium fontanum* are invasive and therefore a conservative measure will only favor the null hypothesis. The remaining eight species exhibit a comparatively short flowering period and do not set seed until flowering has ceased; reported fecundity is therefore considered an accurate measure of annual fecundity per individual.

In accordance with Burns *et al.* (2013) seed number was used to measure fecundity. To determine individual fecundity the number of seed capsules/ racemes per plant was counted. A representative sample of single seed capsules/ racemes were collected from 30 individuals per species, and seeds counted using an Elmor C1 seed counter. The average number of seeds per fruit/ raceme was then calculated. Individual fecundity was determined by multiplying average seed number per fruit/ raceme by the number of fruits per plant.

Data Analysis

Exploratory analysis (mixed-effects model of log seed number against log basal stem diameter, rosette diameter and rosette perpendicular diameter, with species identity as a random effect) revealed basal stem diameter to be the best correlate of fecundity for all species; we therefore used basal stem diameter to represent plant size in all subsequent data analysis. To determine whether invasive species were larger than their native non-invasive relatives, we used generalised linear mixed-effects models (GLMM) with ‘species pair’ as a random effect, ‘species’ and ‘quadrat’ as nested random effects, ‘basal stem diameter’ as a Gaussian response variable, and ‘invasive status’ as a fixed effect. To determine whether invasive species were more fecund we used the same modelling framework but with log-transformed seed number as the Gaussian-distributed response variable. The nesting of the random effects is crucial in this design: measures of size and fecundity for each individual plant are pseudoreplicates that contribute to the means for each species in each phylogenetic pair. The nested models correctly tested the influence of invasiveness on mean traits in each pair. To determine whether, for a given size, invasive species exhibit higher fecundity than their native non-invasive relatives, again we used the same modelling framework, but with ‘invasive status’ and ‘basal stem diameter’ as fixed effects. We tested the impact of invasive status and basal stem diameter on seed set, using likelihood ratio tests between models that included or excluded the “invasiveness” fixed effect.

To determine whether invasive species were more likely to make seed than their non-invasive relatives, we used the same modelling framework, but with “attempt to set seed” as a binary response variable: each plant either flowered and produced seed, or did not. All analyses were performed using the lme4 package (Bates *et al.* 2014) in RStudio Version 0.97.551 (R Core Team 2014). Model checks, following log-transformation of seed number and basal stem diameter, confirmed homoscedasticity and Normality of standardised residuals in all analyses.

Results

Invasive species had significantly larger basal stem diameters than their non-invasive relatives ($\chi^2 = 4.4487$, d.f. = 1, $P = 0.035$) (Fig. 1a). All pairs exhibited this relationship (Fig. 2a).

Across all species basal stem diameter was positively correlated with fecundity ($\chi^2 = 230.62$, d.f. = 1, $P < 0.001$) (Fig. 3). We found that invasive species exhibit significantly higher fecundity than their non-invasive relatives ($\chi^2 = 6.3753$, d.f. = 1, $P = 0.012$ (Fig. 1b). We also found that invasive species exhibit significantly higher fecundity per-unit-size than their non-invasive relatives ($\chi^2 = 4.2286$, d.f. = 1, $P = 0.039$; Fig.1c). When considering the raw data, four out of five of our congener / confamilial pairs exhibited this relationship (Fig. 2b & 2c). The fifth confamilial pair (Scrophulariaceae) did not fit the overall pattern: for a given basal stem diameter the non-invasive species *Pedicularis sylvatica* exhibited higher fecundity than its invasive relative *Rhinanthus minor subsp. minor* (Fig. 2c). Note, however, that a greater proportion of the population of the invasive *R. minor subsp. minor* set seed (Fig. 2d).

Finally, we found that, across phylogenetic pairs, invasive species do not attempt to make seed more frequently than their native, non-invasive relatives ($\chi^2 = 0.1726$, d.f. = 1, $P = 0.678$; Fig. 1d).

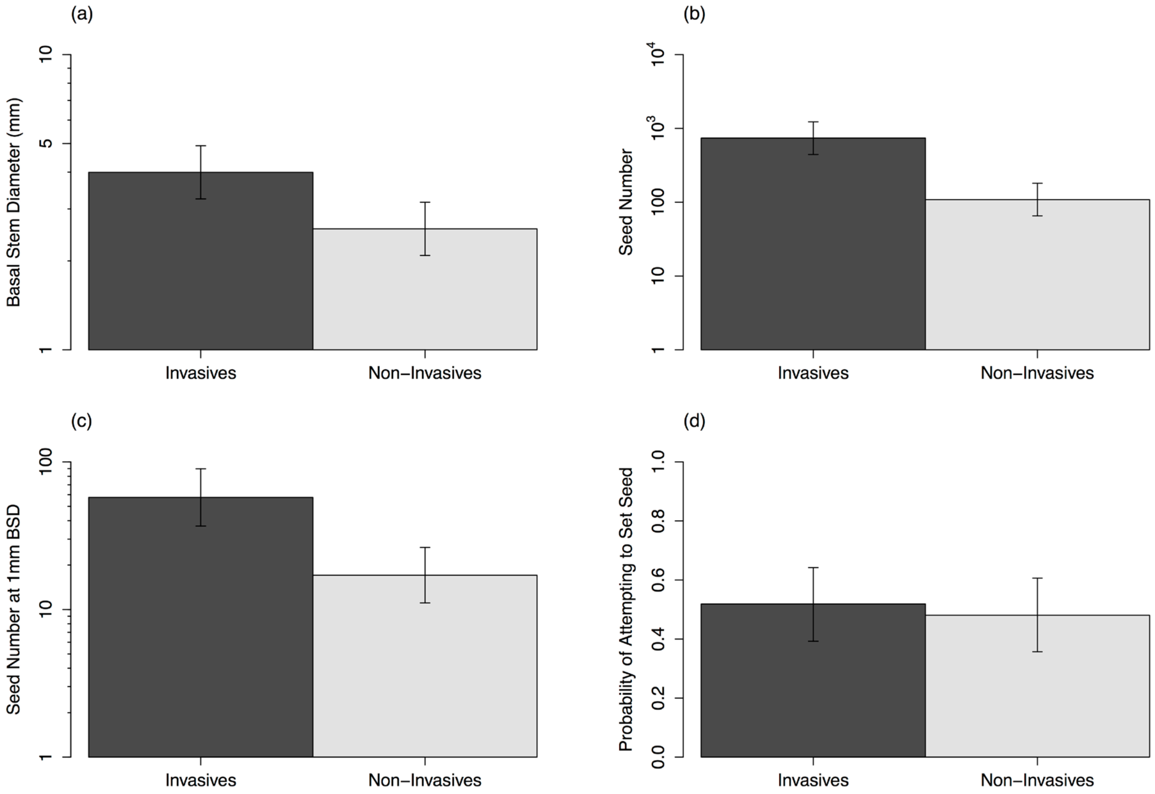

Figure 1. Differences in phenotypic and demographic traits between invasive and non-invasive species, in the native range (Chapter 2). Bars show mean traits (+/- standard error bars) derived from hierarchical mixed effects models, controlling for phylogenetic pairing and averaged across pseudoreplicates within species. a) basal stem diameter for invasive (black bar) and non-invasive (grey bar) species; b) seed number for invasive and non-invasive species; c) seed number for invasive and non-invasive species at a 1mm basal stem diameter (BSD); and d) probability of invasive and non-invasive species attempting to set seed. The y-axis of figure 1a – 1c is on a log scale.

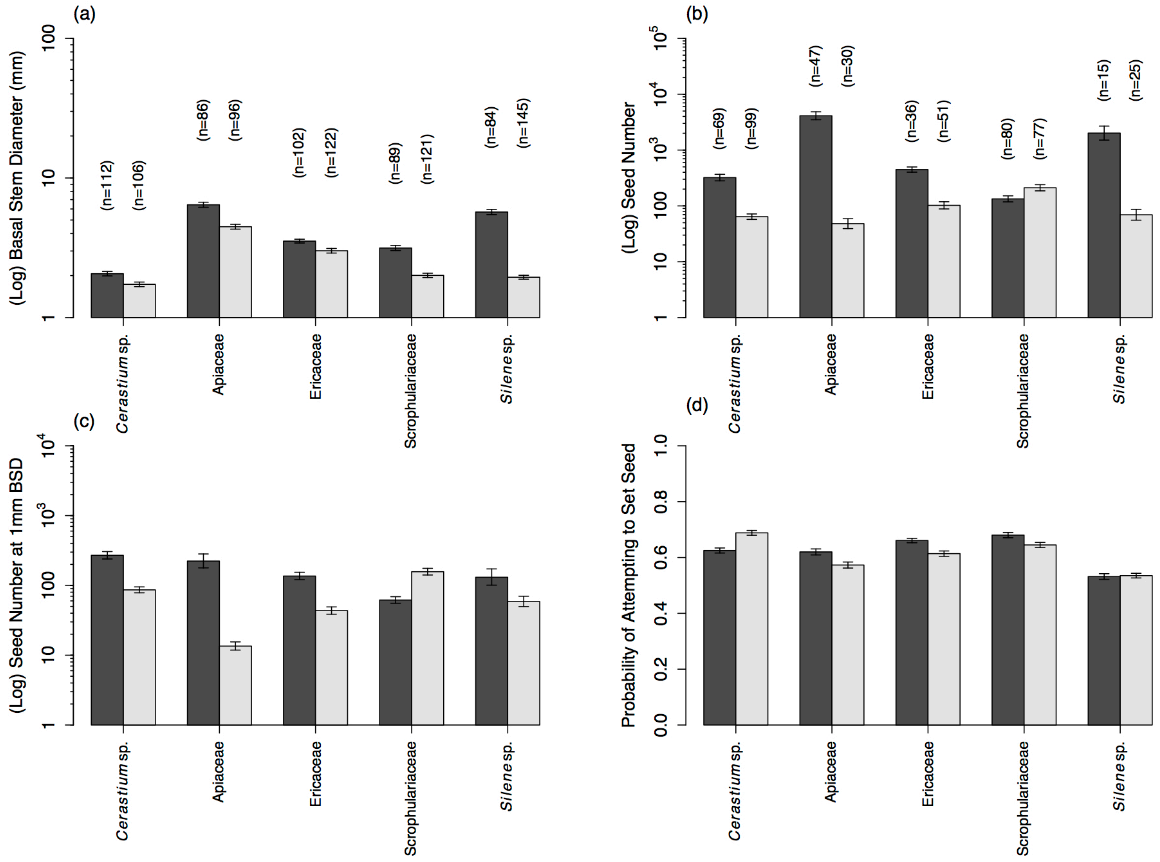

Figure 2. Differences in phenotypic and demographic traits between invasive and non-invasive species, in the native range (Chapter 2). Bars show mean traits (+/- standard error bars) for each species; ‘n’ represents the number of individuals sampled. a) mean (log) basal stem diameter for invasive (black bar) and non-invasive (grey bar) species within each congener/ confamilial pair; b) mean (log) seed number for invasive and non-invasive species within each congener/ confamilial pair; c) mean (log) seed number (fecundity) for invasive and non-invasive species within each congener / confamilial pair at a 1mm basal stem diameter; and d) probability of invasive and non-invasive species within each congener/ confamilial pair attempting to set seed. The y-axis of figure 2a – 2c is on a log scale.

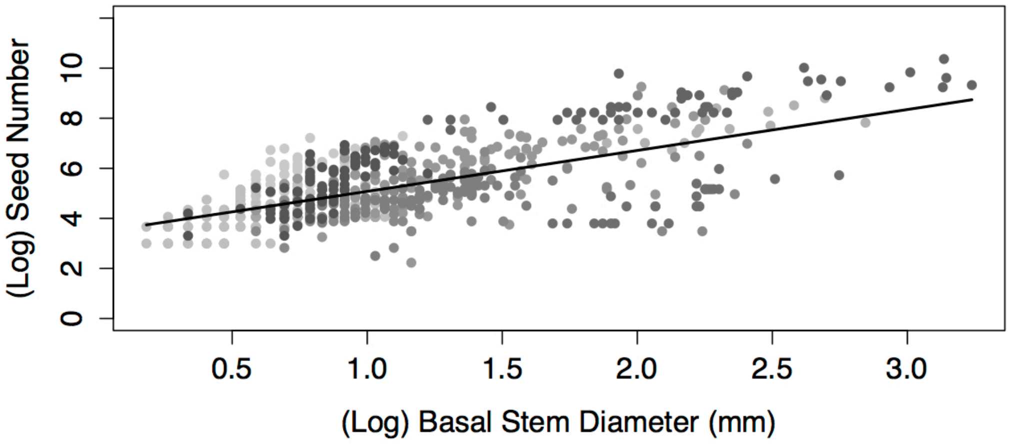

Figure 3. The relationship between basal stem diameter and fecundity (Chapter 2). Points represent measurements of individual plants. Members of each confamilial pair share the same grayscale shading. Fitted line represents a common slope across species and a single intercept for the "average" species.

Discussion

Biological plant invasions are both economically (Pimentel, Zuniga & Morrison 2005) and ecologically costly (Vilà *et al.* 2011) and so there is considerable impetus to identify predictors of invasiveness. By measuring fecundity, size and population structure for five sympatric congener/ confamilial pairs in the native range, we tested four hypotheses: that invasive plant species 1) are larger; 2) are more fecund; 3) exhibit higher fecundity for a given size; and 4) attempt to make seed more frequently, than their non-invasive relatives in the native range.

We confirmed three of our four hypotheses; invasive plant species are larger, more fecund, and more fecund per-unit-size, than their native, non-invasive relatives. Hypothesis 4 was rejected: invasive species do not attempt to make seed more frequently than their native, non-invasive relatives. Our findings, and those of comparative studies in the invaded range (Burns 2006; Mason *et al.* 2008; Moravcová *et al.* 2010; Burns *et al.* 2013), support Baker's (1965) postulation that invasive/ weedy species are likely to grow faster and be more fecund. However, unlike other comparative studies, we also considered the effect of plant size on fecundity. Plant size is important because we know that within a species, larger individuals typically exhibit higher fecundity (Weiner *et al.* 2009) and because increased plant height, larger specific leaf area (Grotkopp, Rejmánek & Rost 2002; Pyšek & Richardson 2007) and biomass (Schlaepfer *et al.* 2010; van Kleunen *et al.* 2011) have been identified as correlates of invasiveness. This raises an important question: are invasive plant species invasive because they are larger (and therefore more fecund) or because they exhibit a constitutively higher fecundity (i.e. higher fecundity per-unit-size) than their non-invasive counterparts? We show that whilst invasive plant species are larger than their native, non-invasive relatives, invasives are also constitutively more fecund. Furthermore, we also consider the effect of population structure on fecundity. Population structure is important because a species exhibiting high individual fecundity but belonging to a population with few reproductive individuals may perform poorly in comparison to a species exhibiting lower individual fecundity but belonging to a population with many reproductive individuals. We find no evidence that invasive species attempt to make seed more frequently than their native non-invading relatives.

Whilst our findings clearly demonstrate that invasive species are larger and exhibit constitutively higher fecundity than their native, non-invading relatives, there is an exception amongst our congener/ confamilial pairs, which deserves discussion. Four of five pairs comprise an invasive species that exhibits higher fecundity than its non-invading relative. The only exception is the Scrophulariaceae pair for which the reverse is true: the non-invasive species *Pedicularis sylvatica* exhibits higher fecundity than its invasive relative *Rhinanthus minor subsp. minor*. One possible explanation pertains to the life form of each congener. *Pedicularis sylvatica*, the non-invading species, is a perennial; therefore whilst this species exhibits higher individual fecundity than its invasive congener, *R. minor subsp. minor,* the invasive congener is an annual that belongs to a population with a higher proportion of reproductive individuals in each growth season. The potential influence of plant breeding system on fecundity also deserves discussion. Several authors have identified autonomous seed production to be an important correlate of invasiveness (Rambuda & Johnson 2004; van Kleunen *et al.* 2008; Hao *et al.* 2011). High fecundity could therefore be correlated with a particular type of breeding system. However, amongst our congeners a greater number of non-invasive species exhibit autonomous seed production; furthermore within species pairs there is considerable overlap in breeding system (Table 1). This indicates that high fecundity is independent of breeding system in this study.

Comparative studies in the invaded range give three possible explanations for high fecundity as correlate of invasiveness (Mason *et al.* 2008; Burns *et al.* 2013): 1) invasives are able to increase allocation to seed production following release from natural enemies or competition; 2) invasives increase allocation to growth following release from natural enemies or competition, with a correlated increase in seed production; and 3) the invaded environment selects for introduced species with a constitutively high fecundity. Environmental variation contributes to significant variation in demographic parameters (Morris & Doak 2005; Buckley *et al.* 2010), therefore measuring demographic parameters in the invaded range cannot distinguish between constituent traits, or trait changes (caused by phenotypic plasticity or microevolution) that are induced by the novel environment. The same principle can be applied to phenotypic traits relating to size (Schlaepfer *et al.* 2010). Consequently, comparative studies in the invaded range (Mason *et al.* 2008; Burns *et al.* 2013) were unable to determine which explanation was most plausible. van Kleunen *et al.* (2011) and Schlaepfer *et al.* (2010) found that invasive species are larger (shoot: root ratio, leaf length and biomass) than their non-invasive relatives in the native range, indicating that larger species are more likely to be invasive. Our results support these findings: we show that invasive species are larger than their non-invasive relatives; however, uniquely we show that invasive species are also constitutively more fecund than their non-invasive relatives in the native range, i.e. prior to any change induced by the novel environment. Our findings suggest that the invaded environment is a biased filter that favours introduced species that are both large and constituently more fecund.

Propagule pressure has been identified as a correlate of invasiveness (Reichard & Hamilton 1997; Herron *et al.* 2007) and it seems probable that inter-regional propagule pressure (the number of dispersal units transported to a new region outside of the native range) is biased; some species are more likely to be transported than other species. We know that plant attractiveness is a correlate of invasiveness (Pyšek & Richardson 2007) so perhaps larger and more fecund plant species are more likely to be transported due to their aesthetic qualities (i.e. inflorescence size) or functionality (i.e. robustness). Evidence for this comes from a positive correlation between inflorescence size and fecundity in the invasive plant *Silene latifolia* (Delph & Herlihy 2012) and from a study of South African Iridaceae. Amongst South African Iridaceae a species is more likely to be naturalised if it is in horticultural use, and taller species are more likely to be used in horticulture (van Kleunen, Johnson & Fischer 2007). Large size may also afford introduced species a competitive advantage over the existing floristic assemblage upon arrival.

The probability of a species colonizing a new site is assumed to increase with the number of dispersal units (seeds or clonal material) produced (Westoby *et al.* 2002). Evidence for this comes from a positive correlation between the number of seeds per plant, amongst naturalised *Crotalaria* species in Taiwan, and species frequency (Wu *et al.* 2005). More frequently occurring, and thus more 'invasive' *Crotalaria* species, are more fecund than their less frequent, naturalised relatives (Wu *et al.* 2005). It therefore seems probable that more fecund species are more likely to be transported to a new region; and once present have a better capacity to spread rapidly due their ability to exert greater local propagule pressure (the number of dispersal units transported within the introduced range). High fecundity may also afford additional, more complex, advantages for invading species. The 'perfect' invasive species is a species that colonises fast, persists and dominates at carrying capacity. Typical trade-offs of colonization and competitive ability are unlikely to be experienced by the 'perfect' invasive species. Classic theory suggests that seed size (and by extension fecundity) is determined by the trade-off between competition and colonization (Turnbull, Rees & Crawley 1999). However, more recently Coomes *et al.* (2002) found that asymmetric competition of co-occurring annual forbs was insufficient to determine seed size; these authors suggest that variation in seed size is more likely to reflect a species' ability to contract and expand its population in response to environmental conditions (Coomes *et al.* 2002; Coomes & Grubb 2003). Smaller seeded and therefore more fecund species, have a greater capacity to 'boom and bust' (Stott *et al.* 2010) in response to environmental conditions and are typically more abundant than larger seeded, less fecund species (Coomes *et al.* 2002; Coomes & Grubb 2003). This suggests that more fecund species have a competitive advantage; however, understanding the relationship between high fecundity and population dynamics is less clear. The emerging study of transient dynamics (short-term dynamics of populations that are not at equilibrium) offers a potential explanation (Townley *et al.* 2007; Stott, Townley & Hodgson 2011).

Transient dynamics of short-term boom and bust have been shown to be exaggerated among species with high fecundity (Stott, Hodgson & Townley 2012). Furthermore, a comparative analysis of the transient population dynamics of 108 plant species identified that populations predicted to grow faster in the long-term exhibit greater potential magnitudes of transient amplification and attenuation (short term increase and decrease respectively relative to asymptotic growth) than slower growing or declining populations (Stott *et al.* 2010). We know that amplification is linked to fecundity (Stott, Hodgson & Townley 2012), and that invasive populations typically grow faster than native or non-invasive populations in the long-term

(Ramula *et al.* 2008; Burns *et al.* 2013). Therefore, perhaps the comparatively high fecundity of invasive populations compared to those of their native non-invading relatives reflects their greater propensity to amplify in the short-term in response to exogenous disturbances, allowing them to colonise vacant niches quickly, coupled with faster population growth in the long-term. This would be consistent with the observation that disturbed environments (those where exogenous disturbances occur more frequently) are more readily invaded than stable ones (D'Antonio, Dudley & Mack 1999; Marvier, Kareiva & Neubert 2004).

Our approach and findings are of direct relevance to the field of invasion biology and ecology. This is the first study to make interspecific comparisons of fecundity as a function of plant size and population structure amongst invasive/ non-invasive congener and confamilial pairs that are representative of multiple life forms. Furthermore, this study is the first to make such comparisons in the native range. Performance in the native range is very important because as invasion biologists / ecologists we are interested in identifying predictors of invasiveness. We know that environmental variation has potential to cause significant variation in demographic parameters and predictions (Morris & Doak 2005; Buckley *et al.* 2010); we therefore suggest that demographic parameters associated with invasiveness in the invaded range are poor predictors of invasiveness, when the objective is to identify potential invaders prior to their introduction.

We acknowledge that our study samples a small number of species pairs, in a restricted geographical area, during one plant growth season. Our findings might therefore be specific to the location of study and the plant assemblage present. Future work should establish whether our findings hold true for a greater number of phylogenetically-paired species that are representative of multiple life forms, and at a global scale. Future work should also test whether invasive populations, exhibiting high fecundity in the native range, grow faster in the long-term than their sympatric, non-invasive, less fecund relatives; determine the importance of other demographic parameters in the growth and decline of invasive and non-invasive populations in the native range; and test the hypothesis that higher fecundity yields greater potential for both transient population amplification in response to disturbance, and long-term population growth.

Author Contributions

The study was conceived by KJ & DH. Data were collected by KJ and were analyzed by KJ & DH. The manuscript was written by KJ & DH with input from IS & RAM.

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Chapter 3:

Jelbert, K., McDonald, R. A. & Hodgson, D. Invasive plants escape the tolerance-fecundity trade-off. In prep. target journal: Oecologia.

Invasive plants escape the tolerance-fecundity trade-off

Abstract

Predicting which plants become invasive, and why, is essential for informing prevention strategies and control programmes. We identified, and sought to explain, a paradox in the ecology of invasive species: high fecundity and propagule pressure are important correlates of invasiveness, and smaller seeded plant species tend to be more fecund than larger seeded species. Small seed mass should therefore be consistently correlated with invasiveness but it is not.

We compared the life history traits of species that are invasive in their non-native range, with the traits of their relatives that have also been introduced but are not invasive. We compared the traits of such paired species living in sympatry in their native range to test four hypotheses: 1) invasive and non-invasive species will not differ in seed mass; but invasive species will exhibit 2) higher reproductive investment (seed production x seed mass); 3) higher reproductive investment per-unit-size; and 4) higher germination probability than their non-invasive relatives.

We find that invasive and non-invasive species do not differ in seed mass or germination probability but that invasive species exhibit higher reproductive investment, and higher reproductive investment per-unit-size than their non-invasive sympatric relatives. This indicates that invasive species escape the typical trade-off of competition and colonization, or of fecundity and tolerance, and exhibit higher fecundity than non-invasive species, without a corresponding reduction in seed mass. High reproductive investment, relative to related species, is an important predictor of invasiveness.

Keywords: Demography, fecundity, invasive, native, reproductive investment, seed mass

Introduction

The ecological and monetary cost of invasive plant species is well documented (Pimentel et al. 2005; Vila et al. 2011). Impacts on native communities range from decreased species richness and reduced fitness of native species (Hejda et al. 2009; Vila et al. 2011) to increased disease transmission, soil erosion and frequency and severity of wildfires (Bradley et al. 2006; Pimentel et al. 2005). For biologists studying and managing invasions, key research objectives are to identify predictors of invasiveness, and their causal mechanisms (Burns et al. 2013; Castro-Díez et al. 2011; Hovick et al. 2012) to inform prevention strategies and control programmes (Hastings et al. 2006; Ramula et al. 2008).

Traits that have been repeatedly identified as correlates of invasiveness in plants include large size (Burns 2006; Castro-Díez et al. 2011; Jelbert et al. 2015; Schlaepfer et al. 2010), high relative growth rate (RGR) (Burns 2006; Grotkopp et al. 2002; van Kleunen et al. 2010), high fecundity (Burns et al. 2013; Jelbert et al. 2015; Mason et al. 2008), greater propagule pressure (Goodwin et al. 1999; Holle and Simberloff 2005), and high germination probability (van Kleunen and Johnson 2007). Overrepresentation of such traits among invasive species is intuitive: high fecundity increases the number of dispersal units (propagules) produced, and therefore the number of dispersal units that are likely to reach new sites (Westoby et al. 2002; Wu et al. 2005). Profuse germination, large size and fast growth promote rapid establishment upon arrival, and subsequently are likely to give a competitive advantage (Schlaepfer et al. 2010; van Kleunen and Johnson 2007).

Seed mass, a trait less consistently associated with invasiveness (Dawson et al. 2011; Mihulka et al. 2003; Schlaepfer et al. 2010; van Kleunen and Johnson 2007) presents a quandary. Several studies identify small seed mass to be a correlate of invasiveness (Graebner et al. 2012; Grotkopp et al. 2002; Hamilton et al. 2005; Rejmánek and Richardson 1996), while others observe no such correlation (Dawson et al. 2011; Mihulka et al. 2003; Schlaepfer et al. 2010; van Kleunen and Johnson 2007). Conversely invasive species can also exhibit larger seed mass than a) their co-occurring native relatives (Daws et al. 2007); and b) introduced non-invasive species (Lake and Leishman 2004) in the introduced range. This irregularity is intriguing because smaller seeded species are typically more fecund than larger seeded species (Coomes and Grubb 2003; Rees and Westoby 1997; Turnbull et al. 1999), and because species exhibiting large fecundity are more likely to be invasive (Jelbert et al. 2015). Theory would therefore predict invasive species to exhibit smaller seed mass than non-invasive species. The literature does not support this prediction (Dawson et al. 2011; Mihulka et al. 2003; Schlaepfer et al. 2010; van Kleunen and Johnson 2007). We postulate that this is because invasive plant species are more fecund for a given seed mass than non-invasive plant species.

Early models of the evolution of offspring mass predict a positive relationship between investment per offspring and offspring success (Lloyd 1987; Smith and Fretwell 1974) but these models do not account for the frequency of competing seed masses, or the effect of the environment on offspring fitness (Rees and Westoby 1997). Classic theory suggests that seed mass (and by extension fecundity) is determined by a trade-off between competition and colonization, or between fecundity and tolerance of stresses (Muller-Landau 2010; Turnbull et al. 1999). These theories describe how larger seeded species, that produce larger and more robust seedlings, are competitively superior (Turnbull et al. 1999) or are better able to tolerate a particular adverse condition or set of conditions (Muller-Landau 2010), but in turn trade off seed size against seed number, and the likelihood of colonizing new sites (Muller-Landau 2010; Turnbull et al. 1999; Westoby et al. 2002). Coomes et al. (2002) found that asymmetric competition alone is insufficient to determine seed size in sympatric annual forbs, and proposed that variation in seed mass is maintained by fluctuating microhabitat heterogeneity (Muller-Landau 2010).

Size at sexual maturity is positively correlated with seed mass (Moles et al. 2004), and is therefore also partially responsible for variation in seed size. This is consistent with Venable (1992) extension of the Smith and Fretwell (1974) model, which predicts that seed mass will increase with increasing maternal resources (i.e. plant size) when seedling survival is low, for instance when offspring fitness is diminished by the frequency of competing seed masses, or by predation. In addition, longevity is also a potential determinant of seed mass, whereby longerlived species exhibit larger seed mass because these species typically require a longer juvenile period to reach maturity, and are therefore expected to require high juvenile survivorship associated with larger seed mass (Moles et al. 2004).

The coexistence of species with varying seed mass is therefore likely attributable to the frequency of competing seed masses (Turnbull et al. 1999), fluctuating microhabitat heterogeneity (Coomes et al. 2002; Muller-Landau 2010), species size, and species longevity (Moles et al. 2004). Whilst the precise mechanism(s) determining seed mass remain poorly understood, what is known is that 1) larger seeds produce larger seedlings (Herrera and Laterra 2009; Turnbull et al. 1999); 2) larger seeded species exhibit higher seedling survival than smaller seeded species (Moles and Westoby 2006; Westoby et al. 2002); and 3) seed mass has been observed to increase between the native and invaded range (Buckley et al. 2003; Daws et al. 2007; Graebner et al. 2012; Hierro et al. 2013). This indicates that larger seeds are advantageous; yet two important correlates of invasiveness (Burns et al. 2013; Jelbert et al. 2015; Mason et al. 2008), high fecundity and propagule pressure, directly trade off against large seed mass (Muller-Landau 2010; Turnbull et al. 1999).

An intuitive explanation is that the ‘perfect’ invasive species escapes the typical trade-offs of competition and colonization or of fecundity and tolerance, and exhibits larger fecundity without an equivalent reduction in seed mass. To our knowledge only one study (Mason et al. 2008) has attempted to test this, revealing that invasive species are more fecund, for a given seed mass, than native species. This influential study has two important shortcomings: 1) Mason et al. (2008) compare reproductive investment of ‘invasive’ species with ‘native’ species, but neglect to exclude species known to be ‘invasive’ elsewhere from the ‘native’ species category. If invasive species are united by an “invasiveness” trait or syndrome, comparisons with species that are invasive elsewhere will conceal or weaken correlates of invasiveness (Jelbert et al. 2015). 2) Mason et al. (2008) source data from the literature and therefore do not account for the effect of environment. This is important because the frequency of competing seed masses (Turnbull et al. 1999) and fluctuating microhabitat heterogeneity (Coomes and Grubb 2003; Coomes et al. 2002; Muller-Landau 2010) are believed to be central to the persistence of multiple seed masses within the same community and because seed mass has been observed to increase between the native and invaded range (Buckley et al. 2003; Graebner et al. 2012; Hierro et al. 2013).

Previously we compared size (basal stem diameter) and fecundity (seed production) of invasive and non-invasive plants in their native range to reveal that invasive species are more fecund per-unit-size than non-invasive species (Jelbert et al. 2015). This work lead directly to our observation of the seed mass – fecundity paradox in the ecology of invasive species, and the objective of this paper, to determine whether invasive plant species escape the seed mass-fecundity trade-off. We use the same wild populations as Jelbert et al. (2015) to ask whether invasive and non-invasive congeners differ in seed mass, reproductive investment (seed production x seed mass) and germination probability. These questions build on the findings of Jelbert et al. (2015) by addressing the unexplored seed mass – fecundity paradox. We hypothesize that 1) invasive and non-invasive plant species will not differ in seed mass, but that invasive plants will exhibit 2) higher reproductive investment; 3) higher reproductive investment per-unit-size; and 4) a higher probability of germination, than their non-invasive sympatric relatives.

Our comparison of sympatric invasive and non-invasive congeners in the native range is crucial to our design: by studying invasive and non-invasive relatives, amongst wild sympatric populations, in the native range (mid and west Cornwall, UK), we can be certain that any correlates identified are not caused by changes that occur during the process of invasion (Jelbert et al. 2015), and that these are not masked by differential selection pressures caused by non-sympatric comparisons.

Methods

Species

Five sympatric congener/ confamilial pairs of wild plant species (Table 1) were selected as described in Jelbert et al. (2015) (Chapter 2). Each pair a) comprised one native species that is invasive elsewhere and one native species that is introduced but non-invasive elsewhere; and b) occurred sympatrically. Sites supporting sympatric species pairs were identified using the ERICA Database held by Dr. Colin French (accessed April 2013). ERICA is a database that holds millions of geo-referenced vascular plant records of the Cornish flora.

Table 1. Species pairs: life form, status, mean seed mass and mean reproductive investment per inflorescence

Family	**Species**	**Common Name**	**Life-Form**	**Mean seed mass**	**Mean Reproductive Investment Per Inflorescence**	**Status**	**Citation**
Caryophyllaceae	*Cerastium fontanum*	Common mouse-ear	Per	0.121	6.271	Invasive	USDA; ISSG
	Cerastium diffusum	Sea mouse-ear	Ann	0.065	1.231	Introduced	USDA
Caryophyllaceae	*Silene dioica*	Red campion	Per	0.967	267.970	Invasive	(Jenkins and Keller 2011); CABI; (Randall 2012)*
	Silene uniflora	Sea campion	Per	0.769	43.808	Introduced	CHAH
Ericaceae	*Calluna vulgaris*	Heather	Shrub	0.032	0.259	Invasive	Australian Invasive Weed List; National Pest Plant Accord; ISSG
	Erica cinerea	Bell heather	Shrub	0.075	1.205	Introduced	CHAH
Scrophulariaceae	*Rhinanthus minor* subsp. *minor*	Yellow rattle	Ann	1.956	21.520	Invasive	(Hulst et al. 1987); CABI; (Randall 2012)*
	Pedicularis sylvatica	Lousewort	Per	0.937	12.186	Introduced	USDA
Apiaceae	*Daucus carota*	Wild carrot	Per	934.000	1104.424	Invasive	USDA
	Eryngium maritimum	Sea holly	Per	44.000	522.886	Introduced	USDA

* Invasive status based on number of citations in the GCWs (Randall 2012)

Plant status was determined by searching invasive species databases, National or State legislation, and by using the following search term in Google '*Latin name* invasive' (accessed April 2013). The following invasive species databases were searched: the Global Invasive Species Database (GISD) http://www.issg.org/database/welcome/, the Invasive Species Compendium (CABI) http://www.cabi.org/isc, the Australian Invasive Weed List http://www.environment.gov.au/biodiversity/invasive/weeds/weeds/lists/index.html, the Australian Plant Census (CHAH) http://www.anbg.gov.au/chah/apc/, the European and Mediterranean Plant Protection Organization (EPPO) database http://www.eppo.int/DATABASES/databases.htm, Schedule 9 of the Wildlife and Countryside Act (1981) http://jncc.defra.gov.uk/page-1377, the United States Department of Agriculture (USDA) Plant Database http://plants.usda.gov/java/noxiousDriver, the National Institute for Environmental Studies (NIES) invasive species of Japan database http://www.nies.go.jp/biodiversity/invasive, and the National Pest Plant Accord http://www.biosecurity.govt.nz/pests/surv-mgmt/mgmt/prog/nppa/list. Species are designated as invasive when described as 'invasive' (also 'weedy' or 'noxious' in the USDA Plant Database) in one or more of the invasive species databases, or when termed 'invasive' by a Government Agency or Academic Institution. Two of our 'invasive' congeners (*Silene dioica* and *Rhinanthus minor subsp. minor*) are listed by CABI as invasive. This status could not be verified from the CABI cited literature but both species are notorious weeds (Hulst et al. 1987; Jenkins and Keller 2011) and have more citations in the Global Compendium of Weeds (GCWs) than their 'non-invasive' congeners (Randall 2012). The number of citations within the GCWs has been used to define global invasive status, and to successively detect correlates of invasiveness (Jenkins and Keller 2011; Schlaepfer et al. 2010). The designation of these species as 'invasive' is therefore considered correct. Species are designated as 'introduced' if naturalized outside of the native range, and as 'native' if listed as such on the Online Atlas of the British and Irish Flora http://www.brc.ac.uk/plantatlas/.

Reproductive Investment

Quadrats were installed for each species at each site. The number of quadrats per species ranged from eight to thirteen (mean = 10). This variation was due to the species area-weighted density and abundance at the site. Quadrats were positioned to capture a representative sample of each sympatric population, and ranged from 0.5 x 0.5m to 1m x 1m in size. Each quadrat was geo-referenced, and permanently marked with buried metal chips, and was relocatable using a Global Positioning System (GPS) to provide an approximate location (accurate to within 10m), and a metal detector to determine the precise location. Individual plants from each population were made relocatable with coloured, biodegradable, hemp string and a unique identification number corresponding to the individual's location. Each plant within each species pair was located on three occasions between late spring and autumn 2013 (May - November), during which plant size (basal stem diameter, rosette diameter and rosette perpendicular diameter), life-stage (i.e. seedling, vegetative, reproductive etc.) and the number of seed capsules/ racemes per plant was recorded. We define basal stem diameter (BSD) as the diameter of the stem at ground level. BSD was measured using 150, 0.1mm precision, dialMax Vernier Dial Calipers. In accordance with Jelbert et al. (2015) we use the term 'plant(s)' to describe an entire plant or, for clonal rhizomatous species, a ramet (Jelbert et al. 2015). With the exception of *S. dioica* and *C. fontanum* the number of seed capsules produced per plant was counted following cessation of flowering (and the possibility of more seed capsules being produced). *S. dioica* and to a lesser extent *C. fontanum* set seed throughout a protracted flowering period exceeding the length of our study. Whilst the reported fecundity measures for these species are considered conservative, both are invasive; our conservative fecundity measure will therefore favour the null hypothesis.

A representative sample of single seed capsules/ racemes were collected from 30 individuals per species, and seeds counted using an Elmor C1 seed counter. Individual fecundity was determined by multiplying the mean number of seeds per capsule/ raceme with the number of seed capsules/ racemes per plant. Collected seeds were air-dried at room temperature for a period of 14 days and dispersal appendages removed prior to being weighed. Seed mass was calculated by weighing 30 seeds per species using a microgram precision balance (Sartorius

MSE3.6P-000-DM). Individual reproductive investment was calculated by multiplying individual fecundity by mean seed mass.

Germination

Transition out of the seed bank was estimated by germination trials. Anecdotal evidence suggests that all of our species require a period of vernalization prior to germination. To replicate minimum winter ground temperatures in the native range, collected, air dried seed was stored at 5°C between collection in Summer 2013, and sowing in January 2014. Seed (n = 300) from each species was split into two trays (n = 150) and sown at a depth of 3mm in a sterile / seed free substrate. Substrate was selected to replicate soil type at each of the five sympatric study sites. This comprised 30% sand and 70% seed compost for those species pairs found in the alkaline soils of the Lizard Peninsula (Ericaceae, Scrophulariaceae, Rosaceae and Caryophyllaceae species); and 70% sand and 30% seed compost for the Apiaceae species pair occurring in dune and strandline habitat. Germination trials were performed in a cold frame located a maximum of 15 miles from each sample population; photoperiod was therefore consistent with the photoperiod experienced by wild plants. Sown seeds were watered (300ml per tray) and the number of germinated seeds counted and removed, every two days between sowing in January and June 2014 inclusive.

Data Analysis

To determine whether invasive species exhibit higher germination probability than their native non-invasive relatives, we used generalised linear mixed-effects models (GLMM) with 'germination' as a binary response variable: each seed either germinated or did not; 'species pair' as a random effect, 'species' as a nested random effect, and 'invasive status' as a fixed effect. The nested model correctly tested the influence of invasiveness on mean traits in each pair; this is crucial to the design because individual plant measures are pseudoreplicates that contribute to the means for each species in each phylogenetic pair. To determine whether invasive species exhibit a significantly different seed mass from non-invasive species, we use the same GLMM modelling framework described previously but with log-transformed "seed mass” as the Gaussian-distributed response variable. To determine whether invasive species exhibit higher reproductive investment than their non-invasive relatives, we used a similar modelling framework, but with log-transformed reproductive investment as the Gaussian-distributed response variable, ‘species pair’ as a random effect, and ‘quadrat’ and ‘species’ as nested random effects. To determine whether invasive species exhibit higher reproductive investment for a given size (basal stem diameter), we use the same modelling framework but with both ‘basal stem diameter’ and ‘invasive status’ as fixed effects. We tested the impact of invasive status and basal stem diameter on reproductive investment, using likelihood ratio tests between models that included or excluded the “invasive” fixed effect. We used basal stem diameter to represent plant size in all of our analyses because previously we find this measure to be the best correlate of fecundity for all species (Jelbert et al. 2015) (Chapter 2). Model checks, following log-transformation of reproductive investment and basal stem diameter, confirmed homoscedasticity and normality of standardised residuals in all analyses. The lme4 package (Bates et al. 2014) in RStudio Version 0.97.551 (R Core Team 2014) was used to perform all analyses.

Results

Invasive and non-invasive species did not differ in seed mass ($\chi^2 = 0.469$, d.f. = 1, $P = 0.49$) (Fig. 1) but invasive species did exhibit a) significantly higher reproductive investment ($\chi^2 = 4.797$, d.f. = 1, $P = 0.029$) (Fig. 2a); and b) significantly higher reproductive investment per-unit-size than their non-invasive relatives ($\chi^2 = 3.900$, d.f. = 1, $P = 0.048$) (Fig. 2b). The raw data shows that all the invasive species exhibit higher reproductive investment than their non-invasive paired relatives (Fig. 3a). This falls to four of five pairs when accounting for their difference in size (Fig. 3b). The confamilial pair (Scrophulariaceae), suggested the reverse relationship; for a given basal stem diameter the non-invasive species *Pedicularis sylvatica* exhibited higher reproductive investment per-unit-size than its invasive relative *Rhinanthus minor subsp. minor* (Fig. 3b).

Finally we found that invasive and non-invasive species did not differ in germination probability ($\chi^2 = 0.428$, d.f. = 1, P = 0.513) (Fig. 4).

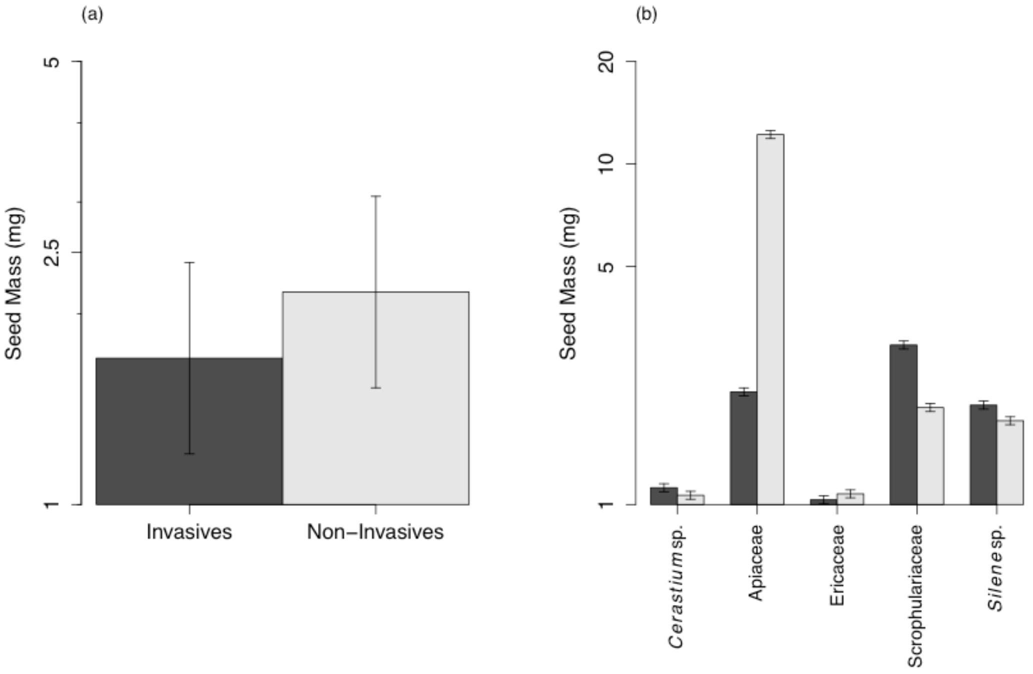

Fig 1. Differences in seed mass between invasive and non-invasive species, in the native range.

a) Mean seed mass (+/- standard error) for invasive (black column) and non-invasive (grey column) species. Means are derived from hierarchical mixed effects models, controlling for phylogenetic pairing and averaged across pseudoreplicates within species. b) Mean seed mass (+/- standard error) for invasive and non-invasive species within each pair. The y-axis of figure 1a – 1b is on a log scale

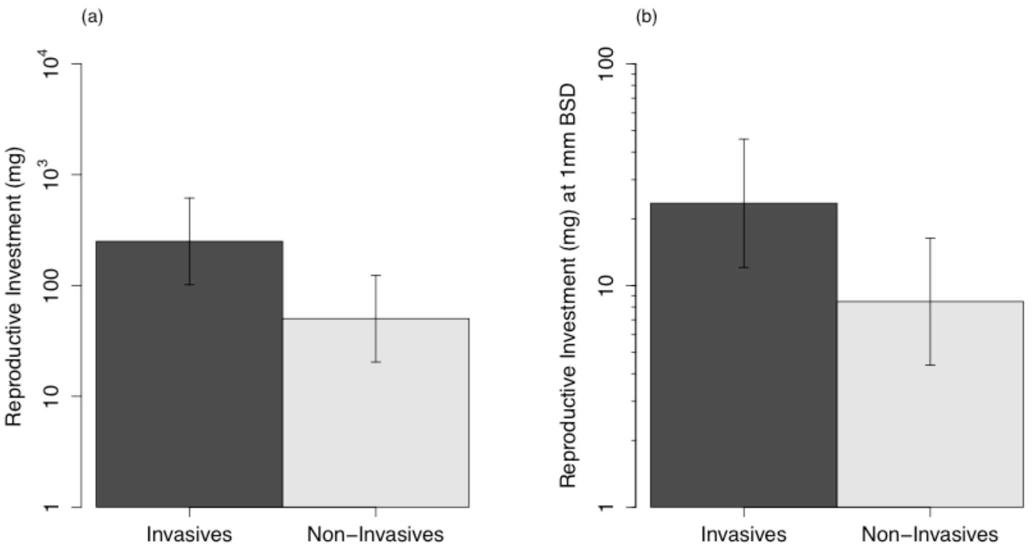

Fig. 2 Differences in reproductive investment between invasive and non-invasive species in their native range. a) Mean (+/- standard error) reproductive investment (milligrams) and b) reproductive investment at a 1mm basal stem diameter. Mean traits are derived from hierarchical mixed effects models, controlling for phylogenetic pairing and averaged across pseudoreplicates within species. The y-axis of figure 2a – 2b is on a log scale

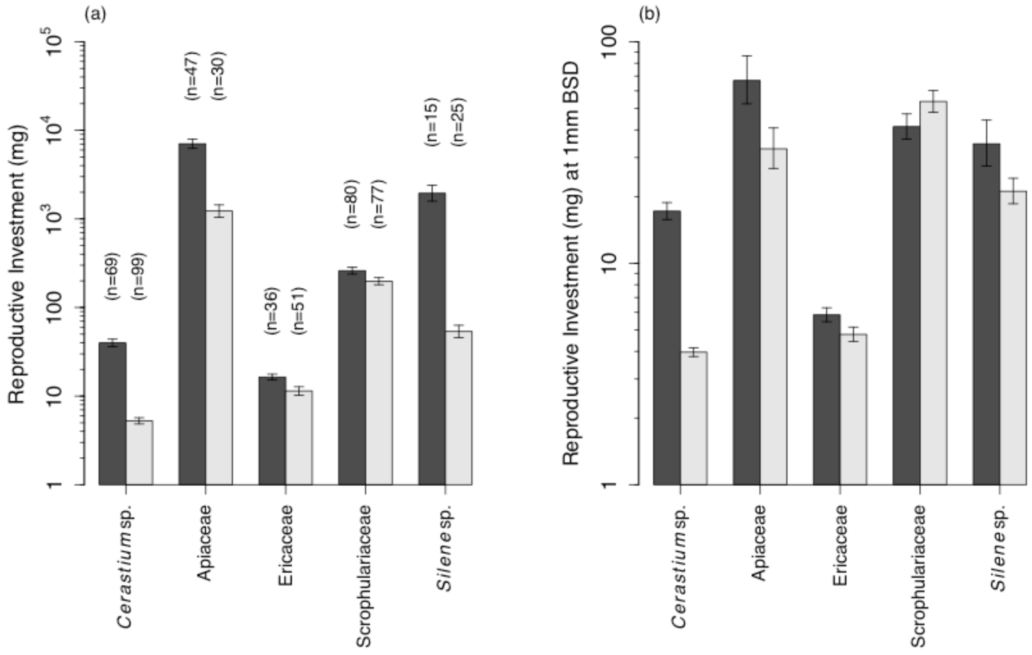

Fig. 3 Differences in reproductive investment between invasive and non-invasive species, in the native range. a) Mean (+/- standard error) reproductive investment for invasive (black column) and non-invasive (grey column) species within each pair. b) Mean reproductive investment for invasive and non-invasive species within each pair at a 1mm basal stem diameter. Sample sizes 'n' represent the number of individuals sampled and are the same in b) as in a)

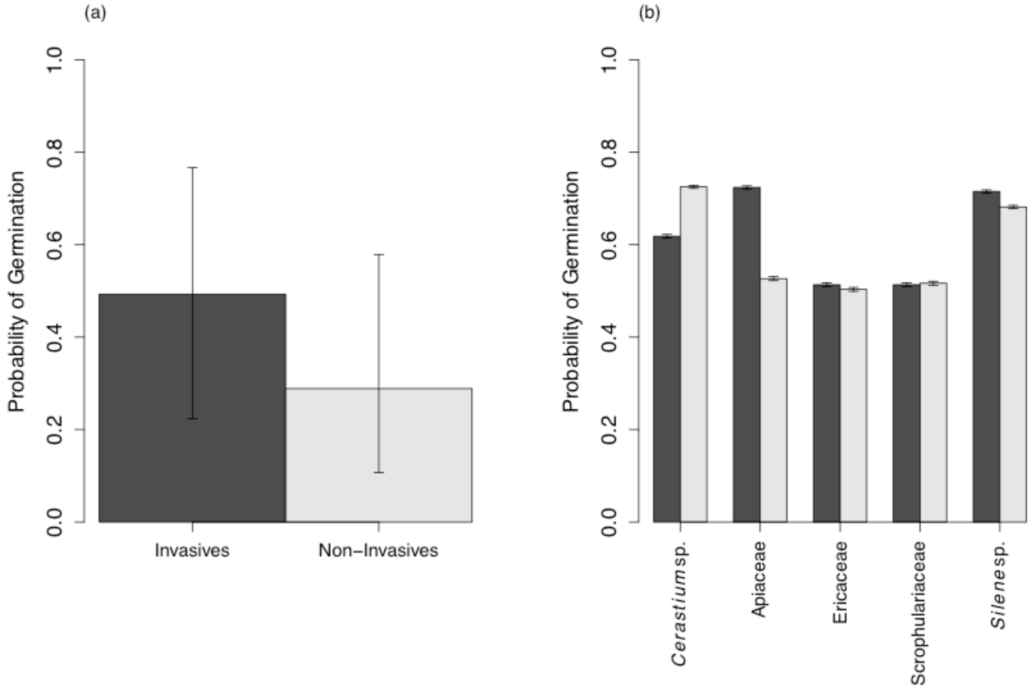

Fig. 4 Differences in germination probability between invasive and non-invasive species, in the native range. a) Mean (+/- standard error bars) germination probability for invasive and non-invasive species; bars show mean traits derived from hierarchical mixed effects models, controlling for phylogenetic pairing and averaged across pseudoreplicates within species. b) Mean (+/- standard error bars) germination probability for invasive (black bar) and non-invasive species (grey bar) within each pair; bars show mean traits for each species

Discussion

We identified a paradox in the ecology of invasive species: if high fecundity and propagule pressure predict invasiveness (Burns et al. 2013; Goodwin et al. 1999; Holle and Simberloff 2005; Jelbert et al. 2015; Mason et al. 2008), and fecundity trades off against seed size (Rees and Westoby 1997; Turnbull et al. 1999), we would predict invasive species to have smaller seeds than non-invasives. This is not the case (Dawson et al. 2011; Mihulka et al. 2003; Schlaepfer et al. 2010; van Kleunen and Johnson 2007).

Here we show that invasive and non-invasive species do not differ in seed mass or germination probability but that invasive species exhibit higher reproductive investment, and higher reproductive investment per-unit-size than their non-invasive sympatric relatives. Our results are in line with Mason et al. (2008) who found that invasive species are more fecund for a given seed mass, than native species; however, unlike Mason et al. (2008) we compare reproductive investment of invasive species with their exported but non-invasive, sympatric relatives in the native range; and control for plant size. By studying invasive and non-invasive congeners/ confamilials amongst sympatric populations in the native range, we can be certain that the correlates identified predict, rather than explain, invasiveness; and that evolutionary pressures determining seed mass are comparable within each species pair.

Plant size is a crucial consideration because larger species exhibit larger seed mass (Moles et al. 2004), larger individuals within a species exhibit higher fecundity (Weiner et al. 2009) and because larger basal stem diameter (Jelbert et al. 2015), biomass (Schlaepfer et al. 2010; van Kleunen et al. 2011), specific leaf area (Grotkopp et al. 2002), and increased plant height (Castro-Díez et al. 2011) are all correlates of invasiveness. We note that Mason et al. (2008) controlled for plant life-form, and that plant size and life-form are unlikely to be independent; however, unlike plant size, life-form has not been consistently correlated with invasiveness (Goodwin et al. 1999). By accounting for plant size, we have shown that invasive species invest more heavily in reproduction and are therefore more fecund for a given seed mass than their non-invasive relatives, even when we account for their difference in size. This indicates that invasive species escape the typical trade-off between competition and colonization, or between fecundity and tolerance, and exhibit higher fecundity than non-invasive species, without a corresponding reduction in seed mass. Furthermore, because we study invasive and non-invasive species in the native range we can be sure that high reproductive investment is a predictor of invasiveness, and not a change that occurs during the process of invasion, potentially as a result of release from natural enemies or competition (Burns et al. 2013; Mason et al. 2008).

Unexpectedly, and in contrast to comparative studies (Schlaepfer et al. 2010; van Kleunen and Johnson 2007), we find that invasive species do not exhibit higher germination probability than their non-invasive relatives. This indicates that high germination probability is not a consistent predictor of invasiveness, and is perhaps regionally specific.

We show very clearly that invasive species, on average, exhibit higher reproductive investment per-unit-size, but there is one exception amongst our species pairs. For the Scrophulariaceae pair, the non-invasive species *Pedicularis sylvatica* exhibits higher reproductive investment per-unit-size than its invasive relative *Rhinanthus minor subsp. minor*. Previously we found that the non-invasive species *Pedicularis sylvatica* exhibits higher fecundity, and higher fecundity per-unit-size than its invasive relative *R. minor subsp. minor*, and attributed this to the life form of each congener (Jelbert et al. 2015). *Pedicularis sylvatica*, the non-invading species, is a perennial; whilst its invasive congener, *R. minor subsp. minor,* is an annual that belongs to a population with a greater number of reproductive individuals per growth season (Jelbert et al. 2015). Interestingly, *R. minor subsp. minor* exhibits higher reproductive investment than the non-invasive *P. sylvatica* when we do not control for plant size.

We propose that the greater reproductive investment of invasive species facilitates invasion in three ways:

1) Propagule pressure is a correlate of invasiveness (Goodwin et al. 1999; Holle and Simberloff 2005). Highly fecund species have a higher probability of being transported

outside of the native range, and once present have a greater ability to spread due to the higher number of propagules produced.

2) Transient dynamics of short-term ‘boom and bust’ are inflated among species with high fecundity (Iles et al. 2016; Stott et al. 2012). Highly fecund species have a superior ability to boom or amplify in response to exogenous disturbances (Stott et al. 2010), and are predicted to exhibit greater long-term population growth than populations of less fecund species (Iles et al. 2016). These demographic traits signify the greater tendency of highly fecund species to amplify in the short-term to exploit vacant niches, whilst achieving fast population growth in the long-term and increased population viability (Iles et al. 2016; Jelbert et al. 2015).
3) The advantages of large seed mass are well documented: larger seeds produce larger seedlings (Herrera and Laterra 2009; Turnbull et al. 1999); and larger seeded species exhibit higher seedling survival than smaller seeded species (Leishman and Westoby 1994; Moles and Westoby 2006; Westoby et al. 2002). Furthermore, seed mass has been observed to increase between the native and invaded range (Buckley et al. 2003; Graebner et al. 2012; Hierro et al. 2013). It is therefore intuitive that seed mass should increase to maximize seedling survival, providing that a corresponding reduction in fecundity is not incurred. Those species that exhibit high reproductive investment will have a better capacity to colonize rapidly, due to the greater number of seeds produced, and their larger mass.

By exploring a paradox in the ecological theory of invasiveness, we reveal that invasive species invest more heavily in reproduction, and are therefore more fecund for a given seed mass than their non-invasive relatives, even when we account for their difference in size. High reproductive investment must convey an advantage for an invading species over those species that invest less in reproduction. However, it is not uncommon for seemingly benign introduced species to behave ‘invasively’, or an acknowledged invasive species to ‘fail’. A plausible explanation is that if, by good fortune, a species reaches a site outside of the native range, the floristic assemblage of the new locality must likely comprise ‘lower reproductive investors’ for the ‘invading’ species to behave ‘invasively’. This situation could explain the global inconsistency of plant status, whereby designated ‘invasive’ species do not behave invasively at every introduced locality. Interestingly, Early and Sax (2014) found that a high proportion of species’ naturalized distribution occurred outside of the climatic conditions inhabited in the native range. This suggests that non-climatic factors, such as competition, play an important role in limiting species’ naturalized distribution (Early and Sax 2014). If this is the case, it seems probable that invasion success is determined by the traits of the ‘invader’ and the traits of the species comprising the recipient community.

We accept that our study samples a small number of phylogenetic species pairs, during one plant growth season, and from a single region of the UK. However, we infer from our results that invasive species are those that successfully produce large numbers of large seeds, and are therefore escapees from the well-established trade-off between fecundity and seed mass. This could help provide management options for the control of established invaders, but could also help identify likely invasives prior to establishment, and recommend their quarantine from international movement or trade. Future work should establish whether our findings hold true at a global scale, for a greater number of phylogenetically-paired species; and establish whether ‘invasive’ (and growing) populations consistently invest more in reproduction than the floristic assemblage, whether introduced or native, of the invaded environment.

Author Contributions

The study was conceived by KJ & DH. Data were collected by KJ and were analyzed by KJ & DH. The manuscript was written by KJ & DH with input from RAM.

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Chapter 4:

Jelbert[a], K., Buss[a], D., McDonald[a], J., Townley[b], S., Franco[c], M., Stott[d], I., Jones[d], O., Salguero-Gómez[e], R., Buckley[f], Y., Knight[ghi], T., Silk[a], M., Sargent[a], F., Rolph[a], S., Wilson[a], P., & Hodgson[a], D. Demographic predictors of invasiveness, among plants. In prep. Target journal: Nature.

Demographic predictors of invasiveness, among plants

Abstract

Invasive plant species are problematic worldwide, threatening native biodiversity, ecosystems, agriculture, industry and human health. Predictive differences between species that become invasive and those that do not, have been difficult to identify, and this uncertainty has led to considerable debate among ecologists. Here we demonstrate that populations of invasive species are better able to recover from disturbance than non-invasive species, even in the native range. This ability to recover is not revealed by standard analyses of stable population growth, which is generally higher in the naturalised range, regardless of invasive status. Recovery from demographic disturbance is a feature of plant life histories with high levels of reproduction, and shows phylogenetic pattern. Our results recommend reproductive capacity as a predictor of invasiveness across the plant kingdom, demonstrate a need for more demographic study of non-invasive plant species, and show great promise as a reliable tool for guiding international policy on trade and movement of plants.

Main Text

Invasive plant species cause problems for native biodiversity, agriculture, industry and human health, worldwide[1-4]. Costs of curtailing the establishment and impact of invasive plants are estimated at £300 billion per annum[5], therefore the halting of further deleterious species introductions is imperative. The question, “Why do some species become invasive, while others do not?”, has been explored widely[3,6,7], but remains largely unanswered[8]. A variety of research approaches[6,8-10] have been used to understand, and predict, the invasion success of plants but there remains no credible or consistent framework that predicts which species will become invasive. Here we focus on species’ population biology (the study of demographic processes that determine population size and structure through time[11]) because a species’ invasiveness is a property of demographic outcomes such as abundance and range size[12], and because phenotypic traits act on invasiveness through their influence on demography[13,14].

Demographic studies have tackled the problem of invasive plants, using functional-trait analyses[7], spread-rate models[9], stage-structured population models to investigate the mechanisms of invasion[6,15-17] and ecosystem-invasibility approaches[10]. Yet remarkably few demographic analyses have employed multi-species comparisons (c.f.[6,15,17]), perhaps in part due to a paucity of accessible demographic data. The emergence and growth of the COMPADRE Plant Matrix Database[18], which currently features >7000 stage-structured demographic models representing almost 700 plant species, means that demographic data is readily accessible and such comparative analyses are now possible.

Any attempt to find predictors of invasiveness must tease apart traits that are features of the species, expressed in the native range as well as the invaded range, from traits that are features of the environment and might therefore differ between native and invaded range. The few multi-species, demographic comparisons between invasive and non-invasive species, undertaken to date, have revealed that invasive populations tend to exhibit a higher population growth rate (λ) than native species in the invaded range[15], and that introduced populations of non-invasive congeners with which they co-occur[6]. Furthermore, fecundity tends to be higher in invasive species[6], relative to non-invasive, introduced species, and to native species in the invaded range[19]. But these comparative studies suffer two critical limitations. First, they focus on demographic features of species in their invaded range. Studying invasive plants in the invaded range conflates predictors of invasiveness with changes that occur during the invasion process[19-21], making it difficult to distinguish between constituent traits and trait changes that are induced by the new environment[14,22]. Demographic parameters and predictions can vary dramatically between habitats, climates and environments[16], and phenotypic traits are known to differ between the native and invaded range (e.g. seed mass[19-21]). Importantly, studies in the invaded range cannot tell us if demographic traits in the native range can be used to predict invasiveness. This information is crucial, if the objective is to identify, quarantine and/or control, potentially ‘invasive’ species before they arrive, establish and spread in a new region. Second, both comparative studies include species in their non-invasive categories that are in fact invasive elsewhere in the world. If there is a shared “invasiveness” trait or syndrome among plants, then failure to exclude invasive species from the non-invasive or native category will weaken or conceal potential predictors of invasiveness.

Here we use a subset of COMPADRE's stage-structured demographic models parameterised with field data from 1,202 plant populations[18] representing a total of 501 plant species, including 29 'invasive' plant species studied in the naturalised range, 32 'invasive' plant species studied in the native range, 126 'naturalized non-invasive' species studied in the native range, 9 'naturalised non-invasive' species studied in the naturalised range and 310 'restricted' plant species studied in the native range[1]. A small number of these species occur in multiple categories. We use these demographies to present a global, demographic comparison of invasive and non-invasive plant species, and the first to control simultaneously for phylogeny and geography (studied in the native or naturalised range). Our objective is to explore links between demography, life history, environment and plant status, to address questions that can explain and predict invasiveness. We ask three main questions. First, is there a demographic syndrome of invasiveness in the native or naturalised range? Second, can invasiveness be predicted using demographic traits in the native range? Third, is invasiveness shared by close relatives (i.e., is there a high phylogenetic signal)?

We use two established metrics of stage-structured demographic models, the stable population growth rate (λ)[23] and demographic inertia (ρ_∞)[24], to compare the projected population dynamics of invasive and non-invasive plants in their native and naturalised ranges. Population projection matrices partition life cycles into distinct life-stages, and contain rates of transition between life stages. These rates of transition are composites of survival, growth and recruitment (the establishment of new individuals per reproductive adult)[23] (Fig. 1A). Populations initiated with a stable stage structure will grow or decline according to the stable growth rate, indefinitely if the environment remains constant and resources are unlimited[23]. The size of populations disturbed away from stable stage structure will amplify or attenuate in the short term, before settling to the stable rate of increase. The long-term impact of this transient dynamic is

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[1] The number of species in each category as listed in the text differs from the number of species listed in the Supplementary Material SM1. The supplementary material is based on the updated analyses and will be used in the published version of Chapter 4.

measured by demographic inertia[24]. In the long-term, non-stable populations will forever be larger or smaller than a population initiated at stable stage structure[24]. Demographic inertia has upper ($\bar{\rho}_{\infty}$) and lower ($\underline{\rho}_{\infty}$) bounds, representing the maximum potential amplification or attenuation of the population following demographic disturbance. Demographic inertia recognises that life-stages vary in reproductive value, hence disturbed populations will either boom or bust relative to the stable growth rate, and the bounds on these responses to disturbance tend to widen with increasing heterogeneity among life-stages and asymmetry among vital rates[25].

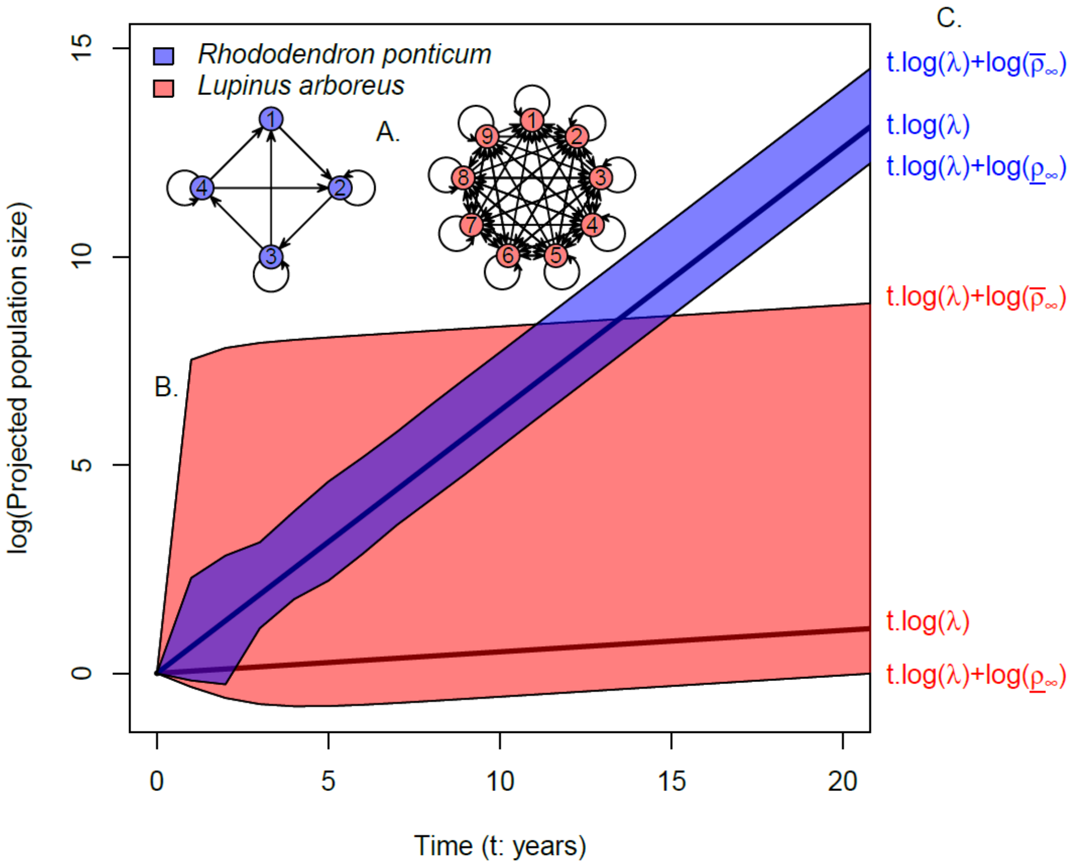

Figure 1: Amplification and attenuation of population size for two invasive plant species. (A) Life cycles of *Lupinus arboreus* and *Rhododendron ponticum* described using discrete life-stages (circles), and rates of transition and per-capita contributions among life-stages (arrows). (B) Projected populations, initiated at unit abundance. Central line for each species projects the stable stage structure, with stable population growth rate λ. Coloured envelopes encapsulate projected transient dynamics caused by disturbed initial stage structures: upper and lower bounds are defined analytically, long-term, by (C) sum of the logs of stable growth and maximal amplification ($\bar{\rho}_\infty$) or attenuation ($\underline{\rho}_\infty$) determined by demographic inertia.

Demographic Syndrome of Invasiveness

We find evidence for a demographic syndrome of invasiveness among plants. Stable rates of population growth (λ) are greater in the naturalised range than in the native range, irrespective of whether a species is classed as introduced or invasive (Fig. 2a). However, invasive plant species exhibit greater potential for demographic amplification ($\bar{\rho}_\infty$) than non-invasive species ('introduced' and 'restricted'), whether measured in the native or naturalised range (Fig. 2b). This suggests that stable population growth rate depends heavily on abiotic or biotic conditions, which can differ between native and naturalised ranges, while the potential to recover from demographic disturbance is a species-level trait that differs between invasive species and non-invasive species. There is little difference in potential demographic attenuation ($\underline{\rho}_\infty$) between invasive and non-invasive plant species (Fig. 2c). We find amplification to correlate strongly and positively with per capita recruitment per lifestage (Fig. 2d), suggesting that high amplification is driven by high rates of recruitment. Finally, we find credible signal of phylogenetic patterns in the residuals of the relationship between demographic amplification and invasiveness (Fig. 3; Online Supplementary Material SM4 Fig. S1), suggesting that the close relatives of invasive plants share demographic traits that might increase their risk of becoming invasive if established outside their native range. We find no such signal of phylogenetic constraints on stable population growth rates.

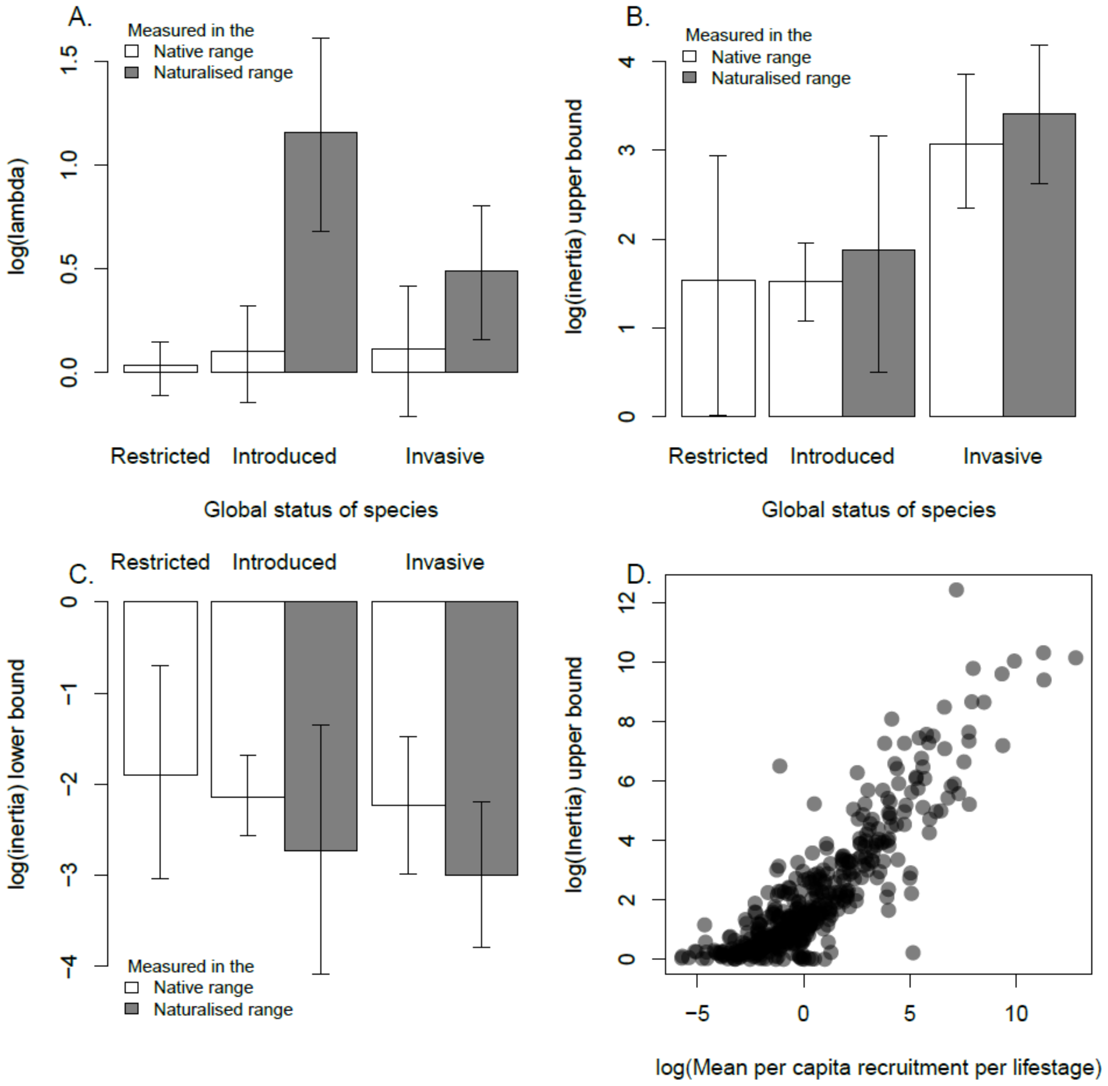

Figure 2: Demographic traits of invasive and non-invasive plant species in the native and naturalised range. Bars show mean demographic trait (+/- 95% Credible Intervals) for restricted, introduced and invasive plants, measured in the respective native or naturalised range; A) stable rate of population increase (mean log (λ)); B) upper bound on demographic inertia (mean $\log(\overline{\rho}_{\infty})$) for invasive and non-invasive plant species; and C) lower bound on demographic inertia (mean $\log(\underline{\rho}_{\infty})$). D) Relationship between upper bound on demographic inertia (mean $\log(\overline{\rho}_{\infty})$) and rates of recruitment (log(mean per capita recruitment per lifestage)).

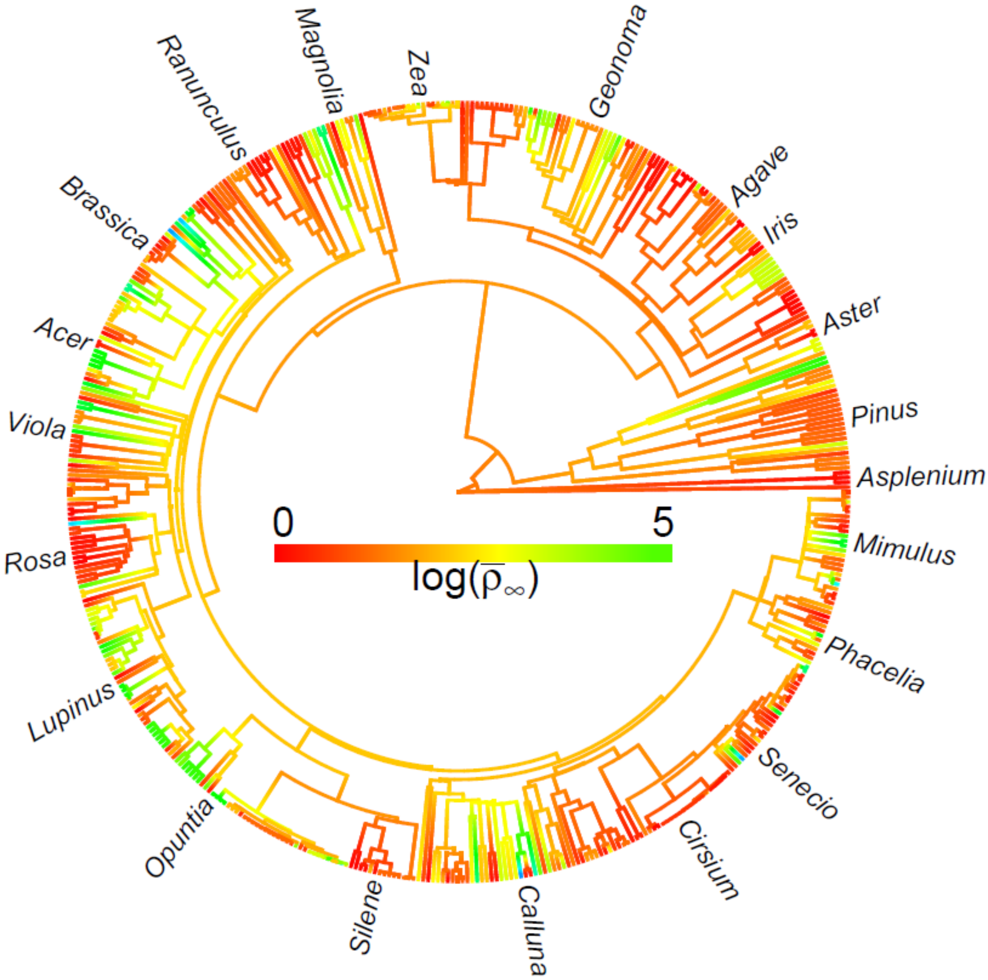

Figure 3: Populations of closely related species share similar potential to recover from demographic disturbance. Phylogram, showing the magnitude of the upper bound on demographic inertia ($\log(\overline{\rho}_\infty)$) and its distribution across the plant Kingdom. Each tip of the phylogeny represents a species in our dataset. For display purposes, only a subset of ‘familiar’ genera are labelled.

Discussion

Invasive species exhibit highest potential for amplification of population sizes in the naturalised range, but crucially also have high amplification in the native range. This finding makes demographic inertia a suitable predictor of invasiveness as opposed to an ‘explanation’ of invasiveness that results from traits changing in the invaded environment[14].

Demographic amplification is a feature of life histories with high, stage-structured rates of recruitment, as demonstrated here and discussed elsewhere[25]. If population structures are biased into certain reproductive life stages following demographic disturbance, then high rates of reproduction can yield rapid recovery via large transient amplification. This is relevant to biological invasions because 1) it is those species with high, stage-structured rates of recruitment that exhibit the highest potential for amplification of population size in response to disturbance[25]; 2) disturbed environments are more readily invaded than stable ones[26]; 3) amplificatory dynamics might promote invasion as populations must grow rapidly to escape Allee effects or demographic stochasticity[27] and 4) populations with greater potential magnitudes of transient amplification are predicted to grow faster in the short-term and remain larger in the long-term[13], and are therefore more likely to become invasive.

A second predictor of demographic amplification is phylogenetic relatedness: closely related plants tend to share similar potential for amplification, which is known to be elevated among species with high recruitment[28]. We attribute this phylogenetic pattern to evolutionary constraints on the morphology of reproductive organs, seed mass and seed production[29]. Recruitment is determined by rates of reproduction and rates of germination and seedling establishment. Reproduction, in turn, is determined by a trade-off between seed mass and seed production[30,31]. Species with larger seeds generally experience greater seedling survivorship but trade-off seed size against the number of seeds produced[30,31]. This phylogenetic patterning is relevant to invasion biology because it suggests that close relatives of invasive plants will, thanks to their sharing of high potential rates of recruitment and therefore demographic amplification, be strong candidates for invasiveness if they establish outside their native range.

Deliberate export of close relatives of known invasives should be avoided.

Stable rates of population growth are greater in the naturalised range than in the native range, irrespective of invasiveness. This means stable population growth has little value as a predictor of invasiveness. However, it yields valuable evidence for fundamental changes in the population biology of plants established outside their native range. Explanations for faster stable population growth in the naturalised range include an escape from native natural pathogens[32], herbivores[33] and competition[34]; environmental filtering such that non-natives are only established in favourable habitats[35]; genotypic filtering such that only vigorous genotypes establish[36]; an adaptive response to the novel environment of the invaded range[37]; and the possibility that populations in the naturalised range are more likely to have been measured during the rapid establishment phase, than native populations. We recommend further research, using comparative demographic analysis, to determine which vital rates are responsible for general increases in stable rates of population increase in naturalised ranges. Counter-intuitively, stable rates of population growth were greatest among non-invasive plants in the naturalised range. We suggest that this might reflect a rapid establishment phase of plant species that have not yet become invasive. Or, it may simply reflect a small sample size of this category of plant species: there has simply been less motivation, or funding available, for the study of long-established and unproblematic populations of non-native species.

An important avenue for future research is to strategically collect demographic data for plant species that represent gaps in our knowledge. Recently, the first global list of naturalised plant species was made showing that 13,168 plant species have naturalized outside of their native range[38]. We have demographic data for only 1.5% (191) of these species. Most of the species that have successfully naturalised have only invaded one or a few regions of the world[39]. There is a critical need for future research to determine if these species with proven naturalisation capacity are likely to become invasive so that measures can be taken to prevent their introduction and to eradicate existing populations in accordance with target 9 of the IUCN 2020 Strategic Plan for Biodiversity. We suggest targeted research to fill in gaps in the phylogeny, global location, and type of plant species (i.e., we need better demographic information on non-invasive alien plants). We also support efforts to rationalize and standardise the various definitions of “invasiveness” in plants[40,41]. Plants can be considered invasive due to their dominance of non-native habitats [42], their impact on native biota of high conservation value[43], their economic impact on ecosystem services or human infrastructure[2,44], or their direct impact on human health[45]. The current lack of a standard, quantifiable definition makes it even more remarkable that we find demographic syndromes that explain or predict invasiveness across the plant kingdom. However, all of these definitions of invasiveness imply that the invasive species is a problem because it persists and spreads, and these are demographic features of the species’ populations, as revealed by our analyses.

We have shown that explanations and predictions of invasiveness are yielded by empirical description of entire life cycles of plant populations growing in native and naturalised ranges. Our comparative database represents a vast amount of work performed by plant ecologists, globally. An important next step is to simplify the task of predicting invasiveness, for future ecologists, managers and policy-makers. It is useful to identify functional traits, or vital rates, that are themselves proxies for population- or species-level invasiveness, especially if they can be measured in the native range, prior to any invasion. We propose that high, stage-structured fecundity is the most important contributor to the link between demographic amplification and invasiveness, and therefore serves as a simple predictor of invasiveness. We also note that phylogenetic signal in demographic amplification might be explained by phenotypic traits that are clearly patterned by evolutionary history among plants: seed size and seed production as determined by the structure of the plant’s reproductive organs[29]. We recommend deeper exploration of links between seed size, seed production, germination, seedling establishment and invasiveness. We recommend that plant species and genera typified by amplificatory life histories, particularly highly fecund species, should not be exported outside their native range.

Methods

Study Species and Populations, and Categorisation:

We extracted all population projection matrices (PPM) from the COMPADRE Plant Matrix

Database (COMPADRE 3.0.0)[18]. We filtered COMPADRE 3.0.0 by including only matrices that described annual or multi-annual timesteps, and excluding matrices generated by pooling data from multiple sites, and those generated for populations reared in the laboratory or greenhouse. We excluded mean matrices when their constituent, individual matrices were available to use instead, and matrices that were reducible[46]. We also checked all PPMs for the 'seed problem'[23], in which the seed/propagule stage class is erroneously assumed to last a full year before germination, and where necessary, corrected these. Projection matrices are commonly parameterised as either "pre-reproductive" (recruitment is measured as fecundity multiplied by rates of germination and seedling survival), or "post-reproductive" (recruitment of seeds measured as adult survival multiplied by fecundity). Post-reproductive matrices tend to have high values of recruitment, which can affect measures of demographic amplification. We therefore converted all post-reproductive matrices to pre-reproductive matrices using algebraic manipulation of vital rates. Finally, we excluded matrices representing populations that had been manipulated experimentally, for example by treatments associated with burning, herbicide, harvesting, grazing or nutrient supplement. The filtered dataset comprised PPMs representing 1,202 spatial populations (many of them replicated through time), representing 501 species of plants.

We classified population status for each PPM as either native, invasive or naturalised, non-invasive at the location of study, and species status as invasive, naturalised but non-invasive outside of the native range, or restricted to the native range. Population status at the study location was identified from the source literature. Species status outside of the native range was determined by searching invasive species databases (Supplementary Material SM1), and by using the following search term in Google '*Latin name* invasive'. Species are considered invasive when designated as 'invasive' (also 'weedy' or 'noxious' in the USDA Plant Database) in one or more of the invasive species databases or when designated as invasive by an Academic Institution or Government Agency. Naturalised status was determined by searching the Global Compendium of Weeds (GCW), and regional floras (Supplementary Material SM1). We define 'naturalised non-invasive' species as those that are naturalized outside of the native range, and ‘restricted’ species as those that are not naturalized. Our refined database includes 29 ‘invasive’ plant species studied in the naturalised range, 32 ‘invasive’ plant species studied in the native range, 126 ‘naturalized non-invasive’ species studied in the native range, 9 ‘naturalised non-invasive’ species studied in the naturalised range and 310 ‘restricted’ plant species studied in the native range[2]. We simplify the categorisation of plant species to be Native or Naturalised (i.e. introduced) at the Study Location; and Restricted (never established outside the native range), Introduced (established outside the native range but not considered invasive), or Invasive (established outside the native range and considered invasive) on a Global Scale.

Demographic metrics from Population Projection Matrices:

The Perron-Frobenius theorem states that the dynamics of a non-negative, irreducible, ergodic projection matrix will, if rates of transition between stages remain constant and growth is not limited, settle from any initial condition to a stable stage structure (relative density of stages in the population) and a stable geometric rate of increase[23]. The stable rate of population increase (λ) is the dominant eigenvalue of a given population projection matrix and the stable stage structure is the normalised, dominant right eigenvector[23]. If the population is initiated at stable stage structure, then the relationship between abundance (N) and time (t) is

$$log(N_t) = log(N_0) + log(\lambda_m).t$$

Demographic inertia (ρ_∞), also known as the Stable Equivalent Ratio[24], measures the long-term impacts of transient population growth or decline caused by disturbance away from stable stage structure[28]. ρ_∞ is the asymptotic ratio of the density of a population disturbed at time zero, to the density of a population initiated at stable stage structure, such that for any initial stage structure:

$$log(N_t) \rightarrow log(N_0) + log(\lambda_{mx}).t + \log(\rho_\infty) \text{ for } t \gg 0$$

ρ_∞ depends on the population’s initial structure, which is usually unavailable in the literature,

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[2] The number of species in each category differs from the number listed in the Supplementary Materials SM1. The supplementary material is based on the updated analyses and will be used in the published version of Chapter 4.

but it has upper and lower bounds that depend only on the projection matrix itself. We measure both upper and lower bounds on inertia for each matrix model, describing the potential for demographic amplification (more population growth than predicted by λ) and demographic attenuation (less population growth than predicted by λ), respectively.

Data Handling and Analysis:

Our filtered database of projection matrices, representing unmanipulated plant populations, included species that were replicated in space and through time. For each replicate spatial population of each species, we averaged the transition rates through time to create a temporal mean matrix. We calculated demographic metrics (stable rate of increase; upper bound on inertia; lower bound on inertia) per population using these temporal mean matrices. We log-transformed these metrics because they describe geometric processes of population growth or decline, then averaged the metrics across populations to yield means per species. We then compared the mean demographic metrics among categories representing where the species was studied (native versus naturalised range) and their global invasiveness status (restricted, introduced or invasive). An alternative approach would be to compare the median of each metric. Here we chose to compare the mean of each metric because throughout our analyses, we logged the demographic measures for each population, and checked the distribution of these values for symmetry. We then analysed the mean of the logs, not the log of the means. The mean of the logs will therefore resemble the median of the logs, and we expect the outcome to be the same.

Species were non-independent due to phylogenetic history. This hierarchical data structure recommended the use of Monte Carlo Markov Chain general linear mixed-effects modelling, implemented using the MCMCglmm package[47] in R[48]. We used the phylogeny associated with the COMPADRE database, derived from Zanne's Plantae phylogeny[49] by authors TK, RS-G and OJ. We set proper uninformative Gamma priors on the error terms associated with residuals, and phylogeny. We included parameter expansion terms for the phylogenetic variance, to avoid issues with model convergence. All models were run for 1 million iterations and satisfied standard MCMC diagnostic tests. Code for analyses is presented in Supplementary Material SM3. Phylogenetic signal in the residuals was diagnosed by posterior distributions of phylogenetic variance that lay credibly above zero. Credibility of differences in demographic metrics among invasiveness categories was determined using MCMC p-values and using overlap of the 95% credible intervals with the means of the posterior distributions of each demographic metric in each category of invasiveness and study-range.

We produced a phylogram that maps the upper bound on demographic inertia through the plant kingdom (Figure 3), using the contMap function in R library phytools version 0.6-00[50]. This function estimates ancestral states using maximum likelihood based on the rerooting of the tree at each internal node.

Robustness of Results:

The results presented here are for Species-level analyses, for which we used mean demographic metrics per species, with phylogenetic control. We chose to present these analyses for simplicity of interpretation. To check robustness of the outcome, we repeated analyses using demographic metrics per population, nested within each species, with the same results. We also extended our analyses to the per-population and per-species projection matrices for “experimentally manipulated” populations in COMPADRE, yielding the same outcomes. We noted that in other analyses of stable and transient population dynamics based on PPMs, that transient metrics (e.g. demographic inertia) can be influenced by the number of lifestages that are used to model structured life cycles. We therefore re-analysed our models with the inclusion of a second predictor: dimension of the PPM itself. Matrix dimension did not influence the magnitude of stable rate of population growth, and its inclusion in the regression models did not affect the significance of the differences between invasiveness categories. Matrix dimension was a significant predictor of demographic inertia but the inclusion of this significant predictor did not affect the significant differences among invasiveness categories (Supplementary Material SM4). Similarly, we reanalyzed our models with inclusion of generation time. Generation time is a predictor of our demographic measures but its inclusion did not influence our results. We chose to present the simplified analyses without inclusion of matrix dimension and generation time.

We performed simple linear mixed-effects modelling of demographic metrics per population per species, and general linear models of metrics per species. These analyses ignored the phylogenetic patterning of the data, but confirmed the results of the MCMCglmm (Supplementary Material SM4). See Supplementary Material SM2 for extended methods. Finally, we calculated the Pseudo R^2 Value to determine the proportion of non-phylogenetic variance that is absorbed by the fixed effect (Supplementary Material SM4). We found that invasion category explained two thirds of the variation in demographic amplification. This provides further evidence of the important links between demographic responses to disturbance, and invasiveness.

Author Contributions

The study was conceived by KJ, and KJ and DH performed the analyses. The phylogeny was provided by TK, OJ & RSG. The manuscript was written by KJ & DH and refined with assistance from the COMPADRE core committee.

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Supplementary Materials

1. List of species and source of species status
2. Supplementary methodological notes
3. R code to replicate the analyses in the paper
4. Supplementary results

Table SM1: List of Species and Source of Species Status

Authors	Journal	Year	DOI_ISBN	Species	Number of populations	Population Status	Species Status	Species Status Source
van Mantgem; Stephenson	J Ecol	2005	10.1111/j.1365-2745.2005.01007.x	Abies concolor	5	native	introduced	http://www.hear.org/gcw/species/abies_concolor/
van Mantgem; Stephenson	J Ecol	2005	0.1111/j.1365-2745.2005.01007.x	Abies magnifica	4	native	introduced	http://www.ars-grin.gov/cgi-bin/npgs/html/taxon.pl?680
Hiura; Fujiwara	J Veg Sci	1999	10.2307/3237309	Abies sachalinensis	2	native	not introduced	restricted
Jiminez-Lobato; Valverde	J Arid Env	2006	10.1016/j.jaridenv.2005.07.002	Acacia bilimekii	1	native	not introduced	restricted
Warton; Wardle	Austral Ecol	2003	10.1046/j.1442-9993.2003.01246.x	Acacia suaveolens	6	native	not introduced	restricted
Tanaka; Shibata; Masaki; Iida; Niiyama; Abe; Kominomi; Nokashizuka	J Veg Sci	2008	10.3170/2007-8-18342	Acer palmatum	2	native	Introduced	http://www.hear.org/gcw/species/acer_palmatum/
Tanaka; Shibata; Masaki; Iida; Niiyama; Abe; Kominomi; Nokashizuka	J Veg Sci	2008	10.3170/2007-8-18342	Acer pictum	2	native	not introduced	restricted
Tanaka; Shibata; Masaki; Iida; Niiyama; Abe; Kominami; Nokashizuka	J Veg Sci	2008	10.3170/2007-8-18342	Acer rufinerve	1	native	Invasive	http://ias.biodiversity.be/species/show/119
Lin; Augspurger	Forest Ecol Manag	2008	10.1016/j.foreco.2008.02.040	Acer saccharum	3	native	Introduced	http://www.hear.org/gcw/species/acer_saccharum/
Easterling; Ellner; Dixon	Ecology	2000	10.1890/0012-9658(2000)081[0694:SSSAAN]2.0.CO;2	Aconitum noveboracense	1	native	not introduced	restricted
Cook; Lyons	PhD thesis	1993	None	Actaea cordifolia	2	native	not introduced	restricted
Mayberry; Elle	Oecologia	2010	10.1007/s00442-010-1809-8	Actaea elata	1	Native	not introduced	Restricted

Authors	Journal	Year	DOI_ISBN	Species	Number of populations	Population Status	Species Status	Species Status Source
Kaye; Pyke	Ecology	2003	10.1890/0012-9658(2003)084[1464:TEOSTO]2.0.CO;2	Actaea elata	3	Native	not introduced	restricted
Froborg; Eriksson	Can J Bot	2003	10.1139/B03-099	Actaea spicata	2	Native	Introduced	http://www.hear.org/gcw/species/actaea_spicata/
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Adenocarpus aureus gibbsianus	1	Native	not introduced	restricted
Wenhui; Yuangang	J For Res	1998	10.1007/BF02856444	Adenophora lobophylla	1	Native	not introduced	restricted
Wenhui; Yuangang	J For Res	1998	10.1007/BF02856444	Adenophora potaninii	1	Native	not introduced	restricted
Cipriotti; Aguiar	Appl Veg Sci	2012	10.1111/j.1654-109X.2011.01138.x	Adesmia volckmannii	1	Native	not introduced	restricted
Ticktin; Nantel	Biol Cons	2004	10.1016/j.biocon.2004.03.019	Aechmea magdalenae	2	Native	not introduced	restricted
Jimenez-Valdes, Godinez-Alvarez, Caballero, Lira	Econ Bot	2010	10.1007/s12231-010-9117-0	Agave marmorata	1	Native	not introduced	restricted
Kiviniemi	Plant Ecol	2002	None	Agrimonia eupatoria	2	Native	introduced	http://www.hear.org/gcw/species/agrimonia_eupatoria/
Hansen; Wilson	J Appl Ecol	2006	10.1111/j.1365-2664.2006.01145.x	Agropyron cristatum	1	invasive	invasive	http://www.esajournals.org/doi/abs/10.1890/10-0631.1
Burns; Pardini; Schutzenhofer; Chung; Seidler; Knight	Ecology	2013	10.1890/12-1310.1	Ailanthus altissima	1	invasive	invasive	http://www.cabi.org/isc/datasheet/3889
Bullock; White; Prudhomme; Tansey; Perea; Hooftman	J Ecol	2011	10.1111/j.1365-2745.2011.01910.x	Ailanthus altissima	1	invasive	invasive	http://www.cabi.org/isc/datasheet/3889
Pfister; Wang	Ecology	2005	10.1890/04-1952	Alaria nana	1	Native	not introduced	restricted
Burns; Pardini; Schutzenhofer; Chung; Seidler; Knight	Ecology	2013	10.1890/12-1310.1	Alliaria petiolata	1	invasive	invasive	http://www.issg.org/database/species/ecology.asp?si=406&fr=1&sts=sss&lang=EN

Authors	Journal	Year	DOI_ISBN	Species	Number of populations	Population Status	Species Status	Species Status Source
Evans; Davis; Raghu; Ragavendran; Landis; Schemske	Ecol Appl	2012	10.1890/11-1291.1	Alliaria petiolata	12	invasive	invasive	http://www.issg.org/database/species/ecology.asp?si=406&fr=1&sts=sss&lang=EN
Kawano; Takada; Nakayama; Hiratsuka	Book	1987	None	Allium monanthum	1	native	not introduced	restricted
Burns; Pardini; Schutzenhofer; Chung; Seidler; Knight	Ecology	2013	10.1890/12-1310.1	Allium sativum	1	introduced	introduced	http://www.hear.org/gcw/species/allium_sativum/
Nault; Gagnon	J Ecol	1993	10.2307/2261228	Allium tricoccum	1	native	not introduced	restricted
Burns; Pardini; Schutzenhofer; Chung; Seidler; Knight	Ecology	2013	10.1890/12-1310.1	Allium vineale	1	invasive	invasive	http://www.hear.org/gcw/species/allium_vineale/
Huenneke; Marks	Ecology	1987	10.2307/1939207	Alnus incana rugosa	2	native	introduced	https://npgsweb.ars-grin.gov/gringlobal/taxonomydetail.aspx?id=2453
Wong; Ticktin	Environ Cons	2014	10.1017/S0376892914000204	Alyxia stellata	5	native	not introduced	restricted
Goldberg; Turner	Ecology	1986	10.2307/1937693	Ambrosia deltoidea	1	native	not introduced	restricted
Miriti; Wright; Howe	Ecol Monog	2001	10.1890/0012-9615(2001)071[0491:TEONOT]2.0.CO;4	Ambrosia dumosa	1	native	not introduced	restricted
Miriti; Wright; Howe	Ecol Monog	2001	10.1890/0012-9615(2001)071[0491:TEONOT]2.0.CO;14	Ambrosia dumosa	1	native	not introduced	restricted
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Anarrhinum fruticosum	1	native	not introduced	restricted
Dostal	J Veg Sci	2007	10.1111/j.1654-1103.2007.tb02519.x	Androsace elongata	5	native	introduced	http://www.hear.org/gcw/species/androsace_elongata/
Williams; Crone	Ecology	2006	10.1890/0012-9658(2006)87[3200:TIOIGO]2.0.CO;2	Anemone patens	1	native	not introduced	restricted

Authors	Journal	Year	DOI_ISBN	Species	Number of populations	Population Status	Species Status	Species Status Source
Cerna; Munzbergova	PLoS ONE	2013	10.1371/journal.pone.0075563	Anthericum liliago	3	native	not introduced	restricted
Cerna; Munzbergova	PLoS ONE	2013	10.1371/journal.pone.0075563	Anthericum ramosum	6	native	introduced	http://www.cabi.org/isc/abstract/20073230836
Marcante; Winkler; Erschbamer	Annals Bot	2009	10.1093/aob/mcp047	Anthyllis vulneraria alpicola	2	native	not introduced	restricted
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Antirrhinum molle lopesianum	1	native	not introduced	restricted
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Antirrhinum subbaeticum	2	native	not introduced	restricted
Zhang; Brockelman; Allen	Biol Cons	2008	10.1016/j.biocon.2008.04.015	Aquilaria crassna	1	native	not introduced	restricted
Stubben	PhD thesis	2007	None	Aquilegia chrysantha	1	native	introduced	https://npgsweb.ars-grin.gov/gringlobal/taxonomydetail.aspx?id=3741
Stubben; Milligan	J Stat Soft	2007	None	Aquilegia sp.	1	NATD	NATD	
Enright; Ogden	Aust J Ecol	1979	10.1111/j.1442-9993.1979.tb01195.x	Araucaria cunninghamii	1	native	introduced	https://npgsweb.ars-grin.gov/gringlobal/taxonomydetail.aspx?id=3837
Enright	Aust J Ecol	1982	10.1111/j.1442-9993.1982.tb01304.x	Araucaria hunsteinii	2	native	not introduced	restricted
Rautiainen; Laine; Aikio; Aspi; Siira; Hyvarinen	Appl Veg Sci	2004	10.1111/j.1654-109X.2004.tb00613.x	Arctophila fulva	2	native	not introduced	restricted
Koop; Horvitz	Ecology	2005	10.1890/04-1483	Ardisia elliptica	5	invasive	invasive	http://www.issg.org/database/species/ecology.asp?si=52&fr=1&sts=sss&lang=EN
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Arenaria grandiflora bolosii	1	native	not introduced	restricted
Dostal	J Veg Sci	2007	10.1658/1100-9233(2007)18[91:PDOAIP]2.0.CO;2	Arenaria serpyllifolia	5	native	introduced	http://www.hear.org/gcw/species/arenaria_serpyllifolia/
Mandujano; Verhulst; Carrillo-Angeles; Golubov	Int J Plant Sci	2007	10.1086/519008	Ariocarpus scaphirostris	1	native	not introduced	Restricted

Authors	Journal	Year	DOI_ISBN	Species	Number of populations	Population Status	Species Status	Species Status Source
Kinoshita	Plant Spp Biol	1987	10.1111/j.1442-1984.1987.tb00030.x	Arisaema serratum	1	native	not introduced	restricted
Bierzychudek	Ecol Monog	1982	10.2307/2937350	Arisaema triphyllum	2	native	introduced	http://www.hear.org/gcw/species/arisaema_triphyllum/
Lefebvre; Chandler-Mortimer	J Appl Ecol	1984	10.2307/2403051	Armeria maritima	1	native	introduced	http://www.hear.org/gcw/species/armeria_maritima/
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Armeria merinoi	2	native	not introduced	restricted
Jakalaniemi	Env and Exp Bot	2011	10.1016/j.envexpbot.2011.03.013	Arnica angustifolia	1	native	introduced	http://www.hear.org/gcw/species/arnica_angustifolia/
Marcante; Winkler; Erschbamer	Annals Bot	2009	10.1093/aob/mcp047	Artemisia genipi	2	native	introduced	http://www.hear.org/gcw/species/arnica_angustifolia/
Damman; Cain	J Ecol	1998	10.1046/j.1365-2745.1998.00242.x	Asarum canadense	4	native	not introduced	restricted
Bell; Bowles; McEachern	Book	2003	978-3-642-07869-9	Asclepias meadii	2	native	not introduced	restricted
Araujo; Serrao; Sousa-Pinto; Aberg	PLoS ONE	2014	10.1371/journal.pone.0092177	Ascophyllum nodosum	3	native	introduced	doi:10.1111/j.1529-8817.2004.04081.x
Aberg	Mar Ecol Prog Ser	1990	10.3354/meps063281	Ascophyllum nodosum	2	native	introduced	doi:10.1111/j.1529-8817.2004.04081.x
Zotz; Schmidt	Biol Cons	2006	10.1016/j.biocon.2005.07.022	Aspasia principissa	1	native	not introduced	restricted
Bucharova; Munzbergova; Tajek	Am J Bot	2010	10.3732/ajb.0900351	Asplenium adulterinum	6	native	not introduced	restricted
Bucharova; Munzbergova; Tajek	Am J Bot	2010	10.3732/ajb.0900351	Asplenium cuneifolium	4	native	not introduced	restricted
Bremer; Jongejans	Popul Ecol	2010	10.1007/s10144-009-0143-7	Asplenium scolopendrium	2	native	not introduced	restricted
Munzbergova	Am J Bot	2007	10.1093/aob/mcm204	Aster amellus	9	native	introduced	http://www.hear.org/gcw/species/aster_amellus/
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Aster pyrenaeus	1	native	not introduced	restricted
Nicole	PhD thesis	2005	None	Astragalus alopecurus	4	native	not introduced	Restricted

Authors	Journal	Year	DOI_ISBN	Species	Number of populations	Population Status	Species Status	Species Status Source
Wall; Hoffmann; Wentworth; Gray; Hohmann	Plant Ecol	2012	10.1007/s11258-012-0068-7	Astragalus michauxii	1	native	not introduced	restricted
Martin; Meinke	Popul Ecol	2012	10.1007/s10144-012-0318-5	Astragalus peckii	2	native	not introduced	restricted
Lesica	Great Bas Nat	1995	10.2307/2445615	Astragalus scaphoides	2	native	not introduced	restricted
Crone; Lesica	Ecology	2004	10.1890/03-0256	Astragalus scaphoides	3	native	not introduced	restricted
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Astragalus tremolsianus	1	native	not introduced	restricted
Kaye; Pyke	Ecology	2003	10.1890/0012-9658(2003)084[1464:TEOSTO]2.0.CO;2	Astragalus tyghensis	5	native	not introduced	restricted
Pinero; Martinez; Sarukhan	Ecology	1984	10.2307/2259545	Astrocaryum mexicanum	4	native	not introduced	restricted
Martinez-Avalos	PhD thesis	2007	None	Astrophytum asterias	5	native	not introduced	restricted
Mandujano; Bravo; Verhulst; Carrillo-Angeles; Golubov	Acta Oeco	2015	10.1016/j.actao.2014.12.004	Astrophytum capricorne	1	native	not introduced	restricted
Zepeda Martinez	thesis	2010	None	Astrophytum ornatum	1	native	not introduced	restricted
Zepeda-Martinez; Manujano; Mandujano; Golubov	J Arid Env	2013	10.1016/j.jaridenv.2012.08.006	Astrophytum ornatum	1	native	not introduced	restricted
Verhulst; Montana; Mandujano; Franco	Oecologia	2008	10.1007/s00442-008-0980-7	Atriplex acanthocarpa	1	native	not introduced	restricted
Verhulst; Montana; Mandujano; Franco	Oecologia	2008	10.1007/s00442-008-0980-7	Atriplex canescens	1	native	introduced	http://www.hear.org/gcw/species/atriplex_canescens/
Hunt	J Appl Ecol	2001	10.1046/j.1365-2664.2001.00586.x	Atriplex vesicaria	9	native	introduced	http://www.hear.org/gcw/species/atriplex_vesicaria/
Lopez-Hoffman; Ackerly; Anten; Denoyer;Ramos	J Ecol	2007	10.1111/j.1365-2745.2007.01298.x	Avicennia germinans	1	native	introduced	http://www.hear.org/gcw/species/avicennia_germinans/
Crone; Marler; Pearson	J Appl Ecol	2009	10.1111/j.1365-2664.2009.01635.x	Balsamorhiza sagittata	1	native	not introduced	restricted

Bradstock; O'Connell	Aust J Ecol	1988	10.1111/j.1442-9993.1988.tb00999.x	Banksia ericifolia	1	native	introduced	http://www.hear.org/gcw/species/banksia_ericifolia/
Zuidema; Boot	J Trop Ecol	2002	10.1017/S0266467402002018	Bertholletia excelsa	2	native	not introduced	restricted
Ebert; Ebert	Vegetatio	1989	10.1007/BF00042253	Betula nana	1	native	introduced	http://www.hear.org/gcw/species/betula_nana/
Lehtila; Tuomi; Sulkinoja	Ecology	1994	10.2307/1939418	Betula pubescens pumila	2	native	introduced	http://www.hear.org/gcw/species/betula_pubescens/
Lesica; Shelly	Am J Bot	1995	10.2307/2445615	Boechera fecunda	3	native	not introduced	restricted
Barot; Gignoux; Vuattoux	J Trop Ecol	2000	10.1017/S0266467400001620	Borassus aethiopum	2	native	introduced	
O'Connor	J Appl Ecol	1993	10.2307/2404276	Bothriochloa insculpta	1	native	introduced	http://www.hear.org/gcw/species/bothriochloa_insculpta/
Fowler; Overath; Pease	Ecology	2006	10.1890/05-1197	Bouteloua rigidiseta	1	native	not introduced	restricted
Noel; Maurice; Mignot; Glemin; Carbonell; Justy; Guyot; Olivieri; Petit	Cons Genet	2010	10.1007/s10592-010-0056-1	Brassica insularis	4	native	not introduced	restricted
Garnier; Lecomte	Ecol Model	2006	10.1016/j.ecolmodel.2005.10.009	Brassica napus	1	NATD	NATD	http://www.hear.org/gcw/species/brassica_napus/
Griffith	Ecology	2010	10.1890/08-1446.1	Bromus tectorum	3	invasive	invasive	http://www.hear.org/gcw/species/bromus_tectorum/
Hernandez-Apolinor; Valverde; Purata	Forest Ecol Manag	2006	10.1016/j.foreco.2005.10.072	Bursera glabrifolia	1	native	not introduced	restricted
Binh	PhD thesis	2009	None	Calamus nambariensis	1	native	NATD	
Binh	PhD thesis	2009	None	Calamus rhabdocladus	1	native	not introduced	restricted
Le Corff; Horvitz	Ecol Model	2005	10.1016/j.ecolmodel.2005.05.009	Calathea micans	1	native	not introduced	restricted
Horvitz; Schemske	Ecol Monog	1995	10.2307/2937136	Calathea ovandensis	2	native	not introduced	restricted
Price; Bowman	J Biogeog	1994	10.2307/2846032	Callitris columellaris	1	native	invasive	http://www.hear.org/pier/species/callitris_columellaris.htm

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Scandrett; Gimmingham	Vegetatio	1989	10.1007/BF00036515	Calluna vulgaris	1	native	invasive	http://www.hear.org/gcw/species/calluna_vulgaris/
van Mantgem; Stephenson	J Ecol	2005	10.1111/j.1365-2745.2005.01007.x	Calocedrus decurrens	3	native	introduced	http://www.hear.org/gcw/species/calocedrus_decurrens/
Chien; Zuidema; Nghia	Popul Ecol	2008	10.1007/s10144-008-0079-3	Calocedrus macrolepis	1	native	not introduced	restricted
Fiedler	J Ecol	1987	10.2307/2260308	Calochortus albus	1	native	not introduced	restricted
Miller; Antos; Allen	PhD thesis	2004	None	Calochortus lyallii	11	native	not introduced	restricted
Fiedler	J Ecol	1987	10.2307/2260308	Calochortus obispoensis	1	native	not introduced	restricted
Fiedler	J Ecol	1987	10.2307/2260308	Calochortus pulchellus	1	native	not introduced	restricted
Fiedler	J Ecol	1987	10.2307/2260308	Calochortus tiburonensis	1	native	not introduced	restricted
Jongejans; Sheppard; Shea	J Appl Ecol	2006	10.1111/j.1365-2664.2006.01228.x	Carduus nutans	3	native	invasive	http://www.cabi.org/isc/datasheet/11259
Shea; Kelly; Sheppard; Woodburn	Ecology	2005	10.1890/05-0195	Carduus nutans	2	native	invasive	http://www.cabi.org/isc/datasheet/11259
Wikberg; Svensson	Plant Ecol	2006	10.1007/s11258-005-9006-2	Carex humilis	2	native	not introduced	restricted
Jongejans; Jorritsma-Wienk; Becker; Dostal; Milden; de Kroon	J Ecol	2010	10.1111/j.1365-2745.2009.01612.x	Carlina vulgaris	4	native	introduced	http://www.hear.org/gcw/species/carlina_vulgaris/
Steenbergh; Lowe	Ecology	1969	10.2307/1933696	Carnegiea gigantea	1	native	not introduced	restricted
Chien; Zuidema; Nghia	Popul Ecol	2008	10.1007/s10144-008-0079-3	Carya sinensis	1	native	not introduced	restricted
Silander	Oecologia	1983	10.1007/BF00379524	Cassia nemophila	1	native	introduced	http://plants.usda.gov/core/profile?symbol=SEARC&mapType=nativity
Davelos; Jarosez	J Ecol	2004	10.1111/j.0022-0477.2004.00907.x	Castanea dentata	6	native	not introduced	restricted

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del Castillo; Trujillo-Argueta; Rivera-Garcia; Gomez-Ocampo; Mondragon-Chaparro	Ecol and Evol	2013	10.1002/ece3.765	Catopsis compacta	1	native	not introduced	restricted
Winkler; Hulber; Hietz	Bas and Appl Ecol	2007	10.1016/j.baae.2006.05.003	Catopsis sessiliflora	1	native	not introduced	restricted
Alvarez-Buylla	Am Nat	1994	10.1086/285599	Cecropia obtusifolia	1	native	invasive	http://www.hear.org/pier/species/cecropia_obtusifolia.htm
Pisanu; Farris; Filigheddu; Begona Garcia	Plant Ecol	2012	10.1007/s11258-012-0110-9	Centaurea horrida	3	native	not introduced	restricted
Jongejans; de Kroon	J Ecol	2005	10.1111/j.1365-2745.2005.01003.x	Centaurea jacea	2	native	invasive	http://www.hear.org/gcw/species/centaurea_jacea/
Emery; Gross	J Appl Ecol	2005	10.1111/j.1365-2664.2004.00990.x	Centaurea podospermifolia	1	introduced	invasive	http://www.hear.org/gcw/species/centaurea_maculosa/
Maines; Knochel; Seastedt	Ecosphere	2013	10.1890/ES13-00094.1	Centaurea stoebe	1	invasive	invasive	https://www.cabi.org/isc/datasheet/12040
Perez-Farrera; Vovides; Octavio-Aguilar; Gonzalez-Astorga; Cruz-Rodriguez; Hernandez-Jonapa; Villalobos-Mendez	Plant Ecol	2006	10.1007/s11258-006-9135-2	Ceratozamia mirandae	1	native	not introduced	restricted
Magda; Duru; Theau	Weed Sci	2004	10.1614/P2202-067	Chaerophyllum aureum	1	native	introduced	http://www.hear.org/gcw/species/chaerophyllum_aureum/
Liu; Menges; Quintana-Ascencio	Ecol Appl	2005	10.1890/03-5382	Chamaecrista lineata keyensis	5	native	not introduced	restricted
Valverde; Hernandez-Apolinor; Mendoza-Amarom	J Sust Forestry	2006	10.1300/J091v23n01_05	Chamaedorea elegans	1	native	invasive	http://www.cabi.org/isc/datasheet/14347
Endress; Gorchov; Robert; Noble	Ecol Appl	2004	10.1890/02-5365	Chamaedorea radicalis	4	native	introduced	http://www.floridata.com/ref/c/cham_rad.cfm

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Berry; Gorchov; Endress; Stevens	Ecology	2008	10.1007/s10144-007-0067-z	Chamaedorea radicalis	1	native	introduced	http://www.floridata.com/ref/c/cham_rad.cfm
Meagher; Antonovics	Ecology	1982	10.2307/1940111	Chamaelirium luteum	3	native	not introduced	restricted
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Cheirolophus metlesicsii	1	native	not introduced	restricted
ter Steege; Boot; Brouwer; Hammond; Vanderhout; Jetten; Khan; Polak; Raaimakers; Zagt	Ecol Appl	1995	10.2307/2269341	Chlorocardium rodiei	1	native	not introduced	restricted
Bullock; White; Prudhomme; Tansey; Perea; Hooftman	J Ecol	2011	10.1111/j.1365-2745.2011.01910.x	Cirsium acaule	1	native	introduced	http://www.hear.org/gcw/species/cirsium_acaule/
Munzbergova	Am J Bot	2005	10.3732/ajb.92.12.1987	Cirsium acaule	1	native	introduced	http://www.hear.org/gcw/species/cirsium_acaule/
Davis; Landis; Nuzzo; Blossey; Gerber; Hinz	Ecol Appl	2006	10.1890/1051-0761(2006)016[2399:DMISOB]2.0.CO;2	Cirsium arvense	1	invasive	invasive	http://www.cabi.org/isc/datasheet/13628
Jongejans; de Vere; de Kroon	Plant Ecol	2008	10.1007/s11258-008-9397-y	Cirsium dissectum	4	native	introduced	http://www.hear.org/gcw/species/cirsium_dissectum/
Ramula	Acta Oeco	2008	10.1016/j.actao.2007.11.005	Cirsium palustre	1	native	introduced	http://www.hear.org/gcw/species/cirsium_palustre/
Munzbergova	Am J Bot	2005	10.3732/ajb.92.12.1987	Cirsium pannonicum	1	native	not introduced	restricted
Dodge	PhD thesis	2005	None	Cirsium perplexans	2	native	not introduced	restricted
Bell; Bowles; McEachern	Book	2003	978-3-642-07869-9	Cirsium pitcheri	1	native	not introduced	restricted

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Ellis; Williams; Lesica; Bell; Bierzychudek; Bowles; Crone; Doak; Ehrlen; Ellis-Adam; McEachern; Ganesan; Latham; Luijten; Kaye; Knight; Menges; Morris; Den Nijs; Oostermeijer; Quintana-Ascencio; Shelly; Stanley; Thorpe; Ticktin; Valverde; Weekley	Ecology	2012	10.1890/11-1052.1	Cirsium pitcheri	3	native	not introduced	restricted
Bell; Powell; Bowles	J Wild Manag	2013	10.1002/jwmg.525	Cirsium pitcheri	1	native	not introduced	restricted
Jolls; Marik; Hamze; Havens	Biol Cons	2015	10.1016/j.biocon.2015.04.006	Cirsium pitcheri	1	native	not introduced	restricted
Dodge	PhD thesis	2005	None	Cirsium scariosum	2	native	introduced	https://npgsweb.ars-grin.gov/gringlobal/taxonomydetail.aspx?id=448120
Dodge	PhD thesis	2005	None	Cirsium tracyi	2	native	not introduced	restricted
Dalgleish; Koons; Adler	J Ecol	2010	10.1111/j.1365-2745.2009.01585.x	Cirsium undulatum	1	native	invasive	http://www.hear.org/gcw/species/cirsium_undulatum/
Bullock; Hill; Silvertown	J Ecol	1994	10.2307/2261390	Cirsium vulgare	2	native	introduced	http://www.hear.org/gcw/species/cirsium_vulgare/
Hegazy	J Arid Env	1990	None	Cleome droserifolia	1	native	introduced	http://www.hear.org/gcw/species/cleome_droserifolia/
DeWalt	Biol Inv	2006	10.1007/s10530-005-5277-8	Clidemia hirta	2	invasive	invasive	http://www.hear.org/gcw/species/clidemia_hirta/
Olmsted; Alvarez-Buylla	Ecol Appl	1995	10.2307/1942038	Coccothrinax readii	1	native	not introduced	restricted
Silva; Trevisan; Estrada; Monosterio	Global Ecol Biogeogr	2000	10.1046/j.1365-2699.2000.00187.x	Coespeletia spicata	1	native	not introduced	restricted
Silva; Trevisan; Estrada; Monosterio	Global Ecol Biogeogr	2000	10.1046/j.1365-2699.2000.00187.x	Coespeletia timotensis	1	native	not introduced	restricted

Winter; Jung; Eckstein; Otte; Donath; Kriechbaum	J Appl Ecol	2014	10.1111/1365-2664.12217	Colchicum autumnale	2	native	introduced	http://hear.org/gcw/species/colchicum_autumnale/
Kalisz; McPeek	Ecology	1992	10.2307/1940182	Collinsia verna	1	native	not introduced	restricted
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Corallorhiza trifida	1	native	not introduced	restricted
Vejdani	PhD thesis	2006	None	Cornus florida	1	native	introduced	http://www.hear.org/gcw/species/cornus_florida/
Lucas; Forseth; Casper	J Ecol	2008	10.1111/j.1365-2745.2007.01350.x	Cryptantha flava	1	native	not introduced	restricted
Prendeville; Tenhumberg; Pilson	New Phyto	2014	10.1111/nph.12730	Cucurbita pepo	3	introduced	introduced	http://plants.usda.gov/core/profile?symbol=CUPE
Boorman; Fuller	New Phyto	1984	10.1111/j.1469-8137.1984.tb03596.x	Cynoglossum officinale	1	native	invasive	http://www.hear.org/gcw/species/cynoglossum_officinale/
Nicole; Brzosko; Till-Bottraud	J Ecol	2005	10.1111/j.1365-2745.2005.01010.x	Cypripedium calceolus	2	native	introduced	http://www.hear.org/gcw/species/cypripedium_calceolus/
Garcia; Goni; Guzman	Cons Biol	2010	10.1111/j.1523-1739.2010.01466.x	Cypripedium calceolus	4	native	introduced	http://www.hear.org/gcw/species/cypripedium_calceolus/
Thorpe; Stanley; Kayne; Latham	Report	2011	None	Cypripedium fasciculatum	3	native	not introduced	restricted
Zhongjian; Rao Wenhui; Liqiang; Yuting	Acta Ecol Sinica	2008	10.1016/S1872-2032(08)60021-9	Cypripedium lentiginosum	1	native	not introduced	restricted
Neubert; Parker	Risk Anal	2004	10.1111/j.0272-4332.2004.00481.x	Cytisus scoparius	14	invasive	invasive	http://www.issg.org/database/species/ecology.asp?si=441&fr=1&sts=sss&lang=EN
Chien; Zuidema; Nghia	Popul Ecol	2008	10.1007/s10144-008-0079-3	Dacrydium elatum	1	native	not introduced	restricted
Sletvold; Oien; Moen	Biol Cons	2010	10.1016/j.biocon.2009.12.017	Dactylorhiza lapponica	2	native	introduced	http://www.cabi.org/isc/datasheet/113786
Binh	PhD thesis	2009	None	Daemonorops poilanei	1	native	not introduced	restricted
Moloney	Ecology	1988	10.3354/meps045001	Danthonia sericea	5	native	introduced	http://www.hear.org/gcw/species/danthonia_sericea/
Verkaar; Schenkeveld	New Phyto	1984	10.1111/j.1469-8137.1984.tb04155.x	Daucus carota	1	native	invasive	https://www.cabi.org/isc/datasheet/18018

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Lin; Miriti; Goodell	Ecol Evol	2016	10.1002/ece3.2163	Dicentra canadensis	3	native	not introduced	restricted
Menges; Quintana-Ascencio; Weekley; Gaoue	Biol Cons	2006	10.1016/j.biocon.2005.08.002	Dicerandra frutescens	7	native	not introduced	restricted
Picard; Mortier; Chagneau	Ecol Model	2010	10.1016/j.ecolmodel.2010.06.010	Dicorynia guianensis	1	native	not introduced	restricted
Zagt; Boot	PhD thesis	1997	None	Dicymbe altsonii	1	native	not introduced	restricted
Sletvold; Rydgren	J Ecol	2007	10.1111/j.1365-2745.2007.01287.x	Digitalis purpurea	1	native	invasive	http://www.hear.org/gcw/species/digitalis_purpurea/
O'Connor	J Appl Ecol	1993	10.2307/2404276	Digitaria eriantha	1	native	invasive	http://www.cabi.org/isc/datasheet/109594
Lazaro-Zermeno; Gonzalez-Espinosa; Mendoza; Martinez-Ramos; Quintana-Ascencio	Forest Ecol Manag	2011	10.1016/j.foreco.2010.10.028	Dioon merolae	2	native	not introduced	restricted
Alvarez-Yepiz; Dovciak; Burquez	Biol Cons	2011	10.1016/j.biocon.2010.08.007	Dioon sonorense	1	native	not introduced	restricted
Castaneda	MSc thesis	2008	None	Dioon spinulosum	2	native	not introduced	restricted
Garcia	Cons Biol	2003	10.1016/S0006-3207(01)00113-6	Dioscorea chouardii	1	native	not introduced	restricted
Werner; Caswell	Ecology	1977	10.2307/1936930	Dipsacus fullonum	11	invasive	invasive	http://www.hear.org/gcw/species/dipsacus_fullonum/
Kawano; Takada; Nakayama; Hiratsuka	Book	1987	None	Disporum sessile	2	native	not introduced	restricted
Kawano; Takada; Nakayama; Hiratsuka	Book	1987	None	Disporum smilacinum	2	native	not introduced	restricted
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Dorycnium spectabile	1	native	not introduced	restricted
Putnam	PhD thesis	2013	None	Draba asterophora	2	native	not introduced	restricted

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Andrello; Bizoux; Barbet-Massin; Gaudeul; Nicole; Till-Bottraud	Cons Biol	2012	10.1016/j.biocon.2011.12.012	Dracocephalum austriacum	7	native	not introduced	restricted
Zagt; Boot	PhD thesis	1997	None	Duguetia neglecta	1	native	not introduced	restricted
Ratsirarson; Silander; Richard	Cons Biol	1996	10.1046/j.1523-1739.1996.10010040.x	Dypsis decaryi	3	native	introduced	USDA
Martorell	Popul Ecol	2007	10.1007/s10144-012-0307-8	Echeveria longissima	1	native	not introduced	restricted
Hurlburt	PhD thesis	1999	None	Echinacea angustifolia	2	native	introduced	http://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:1174497-2
Dalgleish; Koons; Adler	J Ecol	2010	10.1111/j.1365-2745.2009.01585.x	Echinacea angustifolia	1	native	introduced	http://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:1174497-2
Jiminez-Sierra; Mandujano; Eguiarte	Biol Cons	2007	10.1016/j.biocon.2006.10.038	Echinocactus platyacanthus	6	native	not introduced	restricted
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Echinospartum ibericum algibicum	1	native	not introduced	restricted
Mortimer	Book	1983	None	Elymus repens	1	native	introduced	http://www.hear.org/gcw/species/elymus_repens/
Raimondo; Donaldson	Biol Cons	2003	10.1016/S0006-3207(02)00303-8	Encephalartos cycadifolius	1	native	not introduced	restricted
Picard; Yalibanda; Namkosserena; Baya	Forest Ecol Manag	2008	10.1016/j.foreco.2008.02.041	Entandrophragma cylindricum	1	native	not introduced	restricted
Chagneau; Mortier; Picard	J R Stat Soc C	2009	10.1111/j.1467-9876.2008.00657.x	Eperua falcata	1	native	not introduced	restricted
Doak	Ecology	1992	10.2307/1941457	Epilobium latifolium	1	native	not introduced	restricted
Watson; Westoby; Holm	J Ecol	1997	10.2307/2960604	Eremophila forrestii	1	native	not introduced	restricted
Watson; Westoby; Holm	J Ecol	1997	10.2307/2960604	Eremophila maitlandii	2	native	not introduced	restricted
Zhang; Wang; Shi	Chin J Plant Ecol	2009	None	Eremosparton songoricum	2	native	not introduced	restricted

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Kouassi; Barot; Gignoux; Bi	J Trop Ecol	2008	10.1017/S0266467408005312	Eremospatha macrocarpa	1	native	not introduced	restricted
Bullock; White; Prudhomme; Tansey; Perea; Hooftman	J Ecol	2011	10.1111/j.1365-2745.2011.01910.x	Erigeron canadensis	1	introduced	invasive	http://www.cabi.org/isc/datasheet/15251
Satterthwaite; Menges; Quintana-Ascencio	Ecol Appl	2002	10.1890/1051-0761(2002)012[1672:ASBPVI]2.0.CO;2	Eriogonum longifolium gnaphalifolium	1	native	not introduced	restricted
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Erodium paularense	2	native	not introduced	restricted
Andrello; Bizoux; Barbet-Massin; Gaudeul; Nicole; Till-Bottraud	Biol Cons	2012	10.1016/j.biocon.2011.12.012	Eryngium alpinum	7	native	not introduced	restricted
Menges; Quintana-Ascencio	Ecol Monog	2004	10.1890/03-4029	Eryngium cuneifolium	8	native	not introduced	restricted
Curle; Stabbetorp; Nordal	Nord J Bot	2007	None	Eryngium maritimum	1	native	introduced	http://www.hear.org/gcw/species/eryngium_maritimum/
Kawano; Takada; Nakayama; Hiratsuka	Book	1987	None	Erythronium japonicum	2	native	not introduced	restricted
Schmalzel; Reichenbacher; Rutman	Madrono	1995	None	Escobaria robbinsiorum	3	native	not introduced	restricted
Ortega-Baes	PhD thesis	2001	None	Escontria chiotilla	2	native	not introduced	restricted
Byers; Meagher	Ecol Appl	1997	10.1890/1051-0761(1997)007[0519:ACODCI]2.0.CO;2	Eupatorium perfoliatum	3	native	introduced	http://www.hear.org/gcw/species/eupatorium_perfoliatum/
Byers; Meagher	Ecol Appl	1997	10.1890/1051-0761(1997)007[0519:ACODCI]2.0.CO;2	Eupatorium resinosum	2	native	not introduced	restricted
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Euphorbia fontqueriana	1	native	not introduced	restricted

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Silva-Matos; Freckleton; Watkinson	Ecology	1999	10.1890/0012-9658(1999)080[2635:TRODDI]2.0.CO;2	Euterpe edulis	1	native	not introduced	restricted
Arango; Duque; Munoz	Int J Trop Biol	2010	10.15517/rbt.v58i1.5222	Euterpe oleracea	2	native	introduced	http://www.hear.org/gcw/species/euterpe_oleracea/
Zuidema	Book	2000	None	Euterpe precatoria	1	native	not introduced	restricted
Otarola; Avalos	Am J Bot	2014	10.3732/ajb.1400089	Euterpe precatoria	2	native	not introduced	restricted
Batista; Platt; Macchiavelli	Ecology	1998	10.2307/176863	Fagus grandifolia	2	native	introduced	http://www.hear.org/gcw/species/fagus_grandifolia/
Gibert; Magda; Hazard	PLoS ONE	2015	10.1371/journal.pone.0139919	Festuca eskia	2	native	not introduced	restricted
Schulze; Rufener; Erharft; Stoll	Popul Ecol	2012	10.1007/s10144-012-0338-1	Fragaria vesca	12	native	invasive	http://www.cabi.org/isc/datasheet/24409
Yonezawa; Kinoshita; Watano; Zentoh	Evol	2000	10.1111/j.0014-3820.2000.tb01244.x	Fritillaria biflora	2	native	not introduced	restricted
Araujo; Serrao; Sousa-Pinto; Aberg	PLoS ONE	2014	10.1371/journal.pone.0092177	Fucus vesiculosus	3	native	not introduced	restricted
Ang; de Wreede	Mar Ecol Prog Ser	1993	10.3354/meps093253	Fucus vesiculosus	1	native	not introduced	restricted
Osunkoya	Biol Cons	2003	10.1016/S0006-3207(02)00417-2	Gardenia actinocarpa	1	native	not introduced	restricted
Floyd; Ranker	Int J Plant Sci	1998	10.1086/297607	Gaura neomexicana coloradensis	9	native	not introduced	restricted
Vieira, Santos	J Phycol	2010	10.1111/j.1529-8817.2010.00924.x	Gelidium sesquipedale	1	native	not introduced	restricted
Oostermeijer; Brugman; de Boer; den Nijs	J Ecol	1996	10.2307/2261351	Gentiana pneumonanthe	1	native	not introduced	restricted
Lennartsson; Oostermeijer	J Ecol	2001	10.1046/j.1365-2745.2001.00566.x	Gentianella campestris	1	native	not introduced	restricted

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Zuidema; de Kroon; Werger	Ecol Appl	2007	10.1890/1051-0761(2007)017[0118:TSBPAR]2.0.CO;2	Geonoma deversa	2	Native	not introduced	restricted
Svenning	Plant Ecol	2002	10.1023/A:1015520116260	Geonoma macrostachys	1	Native	not introduced	restricted
Rodriguez-Buritica; Orjuela; Galeano	Forest Ecol Manag	2005	10.1016/j.foreco.2005.02.052	Geonoma orbignyana	1	Native	not introduced	restricted
Souza; Martins	Aust Ecol	2006	10.1111/j.1442-9993.2006.01650.x	Geonoma pohliana weddelliana	3	Native	not introduced	restricted
Sampaio; Scariot	J Trop Ecol	2010	10.1017/S0266467409990599	Geonoma schottiana	1	Native	not introduced	restricted
Ramula; Toivonen; Mutikainen	Int J Plant Sci	2007	10.1086/512040	Geranium sylvaticum	3	Native	introduced	http://www.hear.org/gcw/species/geranium_sylvaticum/
Weppler; Stoll; Stocklin	J Ecol	2006	10.1111/j.1365-2745.2006.01134.x	Geum reptans	2	Native	not introduced	restricted
Kiviniemi	Plant Ecol	2002	None	Geum rivale	1	Native	introduced	http://www.hear.org/gcw/species/geum_rivale/
Levine; McEachern; Cowan	J Ecol	2008	10.1111/j.1365-2745.2008.01375.x	Gilia tenuiflora hoffmannii	1	Native	not introduced	restricted
Engel; Aberg; Gaggiotti; Destombe; Valero	J Ecol	2001	10.1046/j.1365-2745.2001.00567.x	Gracilaria gracilis	2	invasive	invasive	GISD
Engel; Aberg; Gaggiotti; Destombe; Valero	J Ecol	2001	10.1046/j.1365-2745.2001.00567.x	Gracilaria gracilis	2	invasive	invasive	GISD
Peters	Book	1991	None	Grias peruviana	1	Native	not introduced	restricted
CITES	Plants Committee	2008	None	Guaiacum sanctum	1	Native	not introduced	restricted
Mondragon	Plant Spp Biol	2009	10.1111/j.1442-1984.2009.00230.x	Guarianthe aurantiaca	1	Native	not introduced	restricted
Loayza; Knight	Ecology	2010	10.1890/09-0480.1	Guettarda viburnoides	3	Native	not introduced	restricted
Rae; Ebert	Int J Plant Sci	2002	10.1086/339719	Harrisia fragrans	2	Native	not introduced	restricted

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Adams; Marsh; Knox	Biol Cons	2005	10.1016/j.biocon.2005.02.001	Helenium virginicum	1	Native	not introduced	restricted
Marrero-Gomez; Oostermeijer; Carque-Alamo; Banares-Baudet	Biol Cons	2007	10.1016/j.biocon.2007.01.010	Helianthemum juliae	1	Native	not introduced	restricted
Iriondo; Albert; Gimenez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Helianthemum polygonoides	1	Native	not introduced	restricted
Iriondo; Albert; Gimenez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Helianthemum teneriffae	1	Native	not introduced	restricted
Nantel; Gagnon	Ecology	1999	10.1046/j.1365-2745.1999.00388.x	Helianthus divaricatus	4	native	introduced	http://www.hear.org/gcw/species/helianthus_divaricatus/
Bruna	Ecology	2003	10.1890/0012-9658(2003)084[0932:APPIFH]2.0.CO;2	Heliconia acuminata	7	native	introduced	http://www.hear.org/pier/species/heliconia_spp.htm
Schleuning; Huaman; Matthies	J Ecol	2008	10.1111/j.1365-2745.2008.01416.x	Heliconia metallica	2	native	invasive	http://www.hear.org/pier/species/heliconia_spp.htm
Nehrbass; Winkler; Pergl; Perglova; Py□sek	Pers Plant Ecol Evol Syst	2006	10.1016/j.ppees.2005.11.001	Heracleum mantegazzianum	1	invasive	invasive	https://www.cabi.org/isc/datasheet/26911
Wells; Rothery; Cox; Bamford	Bot J Lin Soc	1998	10.1111/j.1095-8339.1998.tb02514.x	Herminium monorchis	1	native	not introduced	restricted
O'Connor	J Appl Ecol	1993	10.2307/2404276	Heteropogon contortus	1	native	invasive	http://www.hear.org/gcw/species/heteropogon_contortus/
Balcazar	PhD thesis	2013	978-90-9027402-7	Heteropsis flexuosa	1	native	not introduced	restricted
Balcazar	PhD thesis	2013	978-90-9027402-7	Heteropsis macrophylla	1	native	not introduced	restricted
Balcazar	PhD thesis	2013	978-90-9027402-7	Heteropsis oblongifolia	1	native	not introduced	restricted
Thomas; Dale	Can J Bot	1975	10.1139/b75-331	Hieracium floribundum	1	invasive	invasive	http://www.hear.org/gcw/species/hieracium_floribundum/
Vega; Montana	Plant Ecol	2004	10.1023/B:VEGE.0000048094.21994.74	Hilaria mutica	2	native	not introduced	restricted

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Pfeifer; Wiegand; Heinrich; Jetschke	J Appl Ecol	2006	10.1111/j.1365-2664.2006.01148.x	Himantoglossum hircinum	1	native	introduced	http://www.hear.org/gcw/species/himantoglossum_hircinum/
Bullock; White; Prudhomme; Tansey; Perea; Hooftman	J Ecol	2011	10.1111/j.1365-2745.2011.01910.x	Himantoglossum hircinum	1	native	introduced	http://www.hear.org/gcw/species/himantoglossum_hircinum/
Baldauf; Correa; Ferreira; Santos	Forest Ecol Manag	2015	10.1016/j.foreco.2015.06.022	Himatanthus drasticus	2	native	not introduced	restricted
Kaye; Benfield	Report	2004	None	Horkelia congesta	1	native	not introduced	restricted
Gross; Lockwood; Frost; Morris	Cons Biol	1998	10.1111/j.1523-1739.1998.97285.x	Hudsonia montana	1	native	not introduced	restricted
Hara; Kanno; Hirabuki; Takehara	J Veg Sci	2004	10.1111/j.1654-1103.2004.tb02286.x	Hydrangea paniculata	1	native	introduced	http://www.hear.org/gcw/species/hydrangea_paniculata/
Sinclair	PhD thesis	2002	None	Hydrastis canadensis	1	native	introduced	http://eol.org/pages/594852/maps
Christensen; Gorchov	Plant Ecol	2010	10.1007/s11258-010-9749-2	Hydrastis canadensis	3	native	introduced	http://eol.org/pages/594852/maps
Okland	Oikos	2000	10.1034/j.1600-0706.2000.880301.x	Hylocomium splendens	1	native	not introduced	restricted
Garnier; Dajoz	J Ecol	2001	10.1890/0012-9658(2001)082[1720:ESOALV]2.0.CO;2	Hyparrhenia diplandra	3	native	not introduced	restricted
Quintana-Ascencio; Menges; Weekley	Cons Biol	2003	10.1046/j.1523-1739.2003.01431.x	Hypericum cumulicola	13	native	not introduced	restricted
Jongejans; de Kroon	J Ecol	2005	10.1111/j.1365-2745.2005.01003.x	Hypochaeris radicata	2	native	invasive	http://www.issg.org/database/species/search.asp?sts=sss&st=sss&fr=1&x=0&y=0&sn=Hypochaeris+radicata&rn=&hci=-1&ei=-1&lang=EN only invasive in La Reunion (island and region of France), has been introduced in the US and falkland islands but is not classified as invasive. GISD
Steets; Knight; Ashman	Am Nat	2007	10.1086/518178	Impatiens capensis	2	native	introduced	http://www.hear.org/gcw/species/impatiens_capensis/ http://alienplantsbelgium.be/content/impatiens-capensis

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Campbell; Waser	Am Nat	2007	10.1086/510758	Ipomopsis tenuituba	1	native	not introduced	restricted
Pinard	Biotrop	1993	10.2307/2388974	Iriartea deltoidea	5	native	not introduced	restricted
Ang; de Wreede; Shaughnessy; Dyck	Hydrobiol	1990	10.1007/978-94-009-2049-1_27	Iridaea splendens	1	native	not introduced	restricted
Burns; Pardini; Schutzenhofer; Chung; Seidler; Knight	Ecology	2013	10.1890/12-1310.1	Iris germanica	1	introduced	invasive	http://www.hear.org/pier/species/iris_germanica.htm
Pathikonda; Ackleh; Hasenstein; Mopper	Cons Biol	2009	10.1111/j.1523-1739.2008.01073.x	Iris hexagona	1	native	not introduced	restricted
Forbes	Weed Res	1977	10.1111/j.1365-3180.1977.tb00498.x	Jacobaea vulgaris	1	native	introduced	http://www.hear.org/gcw/species/senecio_jacobaea/ brc.ac.uk
Couralet; Sass-Klaassen; Sterck; Bekele; Zuidema	Forest Ecol Manag	2005	10.1016/j.foreco.2005.05.065	Juniperus procera	1	native	not introduced	restricted
Iriondo; Albert; Gimenez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Jurinea fontqueri	1	native	not introduced	restricted
Gaoue; Ticktin	Cons Biol	2010	10.1111/j.1523-1739.2009.01345.x	Khaya senegalensis	6	native	invasive	http://www.hear.org/pier/species/khaya_senegalensis.htm
Pino; Pico; Roa	Bot J Lin Soc	2007	10.1111/j.1095-8339.2007.00628.x	Kosteletzkya pentacarpos	1	native	introduced	http://www.iucnredlist.org/details/161916/0
Kouassi; Barot; Gignoux; Bi	J Trop Ecol	2008	10.1017/S0266467408005312	Laccosperma secundiflorum	1	native	not introduced	restricted
Bullock; White; Prudhomme; Tansey; Perea; Hooftman	J Ecol	2011	10.1111/j.1365-2745.2011.01910.x	Lactuca serriola	1	native	invasive	http://www.hear.org/gcw/species/lactuca_serriola/
Chapman	Hydrobiol	1993	10.1007/978-94-011-1998-6_31	Laminaria digitata	1	native	not introduced	restricted
Osunkoya; Perrett; Fernando; Clark; Raghu	Popul Ecol	2013	10.1007/s10144-013-0364-7	Lantana camara	2	invasive	invasive	http://www.issg.org/database/species/ecology.asp?si=56&fr=1&sts=sss&lang=EN

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Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Laserpitium longiradium	1	native	not introduced	restricted
Ehrlen	J Ecol	1995	None	Lathyrus vernus	9	native	introduced	http://www.ars-grin.gov/cgi-bin/npgs/html/tax_search.pl?Lathyrus%20vernus
Maliakal Witt	PhD thesis	2004	None	Lechea cernua	2	native	not introduced	restricted
Maliakal Witt	PhD thesis	2004	None	Lechea deckertii	2	native	not introduced	restricted
Keller; Vittoz	Alp Botany	2015	10.1007/s00035-014-0142-y	Leontopodium nivale alpinum	2	introduced	introduced	Sell, P. and Murrell, G. (2006) Flora of Great Britain and Ireland: Volume 4, Campanulaceae - Asteraceae. University of Cambridge
Tremblay; Ackerman	Biol J Linn Soc	2001	10.1006/bijl.2000.0485	Lepanthes eltoroensis	3	native	not introduced	restricted
Tremblay; Ackerman	Biol J Linn Soc	2001	10.1006/bijl.2000.0485	Lepanthes rubripetala	6	native	not introduced	restricted
Tremblay; Ackerman	Biol J Linn Soc	2001	10.1006/bijl.2000.0485	Lepanthes rupestris	7	native	not introduced	restricted
Tremblay; McCarthy	PLoS ONE	2014	10.1371/journal.pone.0102859	Lepanthes rupestris	7	native	not introduced	restricted
Bernatus	Report	1995	None	Lepidium davisii	6	native	not introduced	restricted
Schutzenhofer; Knight	Ecol Appl	2007	10.1890/06-1282	Lespedeza juncea sericea	1	invasive	invasive	http://www.issg.org/database/species/ecology.asp?si=270&fr=1&sts=sss&lang=EN
Swab	PhD thesis	2014	None	Leucopogon setiger	1	native	not introduced	restricted
Ellis	Ecology	2012	10.1890/11-1052.1	Liatris scariosa	3	native	not introduced	restricted
Baltzer; Reekie; Hewlin; Taylor; Boates	Can J Bot	2002	10.1139/b02-070	Limonium carolinianum	1	native	not introduced	restricted
Hegazy	J Appl Ecol	1992	10.2307/2404462	Limonium delicatulum	1	native	not introduced	restricted
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Limonium erectum	1	native	not introduced	restricted
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Limonium geronense	1	native	not introduced	restricted
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Limonium malacitanum	1	native	not introduced	restricted

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Vejdani	PhD thesis	2006	None	Lindera benzoin	1	native	introduced	http://www.hear.org/gcw/species/lindera_benzoin/
Hara; Kanno; Hirabuki; Takehara	J Veg Sci	2004	10.1111/j.1654-1103.2004.tb02286.x	Lindera umbellata	1	native	not introduced	restricted
Verkaar; Schenkeveld	New Phyto	1984	10.1111/j.1469-8137.1984.tb04155.x	Linum catharticum	1	native	introduced	http://www.hear.org/gcw/species/linum_catharticum/
Munzbergova	Plant Biology	2013	10.1111/plb.12007	Linum flavum	3	native	not introduced	restricted
Munzbergova	Plant Biology	2013	10.1111/plb.12007	Linum tenuifolium	3	native	introduced	http://www.hear.org/gcw/species/linum_tenuifolium/
Bricker; Maron	Ecology	2012	10.1890/11-0948.1	Lithospermum ruderale	3	native	not introduced	restricted
Lacey; Royo; Bates; Herr	Castanea	2001	None	Lobelia boykinii	3	native	not introduced	restricted
Pico; de Kroon; Retano	Ecology	2002	10.1890/0012-9658(2002)083[1991:AEFAFS]2.0.CO;2	Lobularia maritima	1	native	introduced	http://www.hear.org/gcw/species/lobularia_maritima/
Kaye; Pyke	Ecology	2003	10.1890/0012-9658(2003)084[1464:TEOSTO]2.0.CO;2	Lomatium bradshawii	1	native	not introduced	restricted
Kaye; Pendergrass; Finley; Kauffman	Ecol Appl	2001	10.1890/1051-0761(2001)011[1366:TEOFOT]2.0.CO;2	Lomatium bradshawii	2	native	not introduced	restricted
Kaye; Pyke	Ecology	2003	10.1890/0012-9658(2003)084[1464:TEOSTO]2.0.CO;2	Lomatium cookii	2	native	not introduced	restricted
Burns; Pardini; Schutzenhofer; Chung; Seidler; Knight	Ecology	2013	10.1890/12-1310.1	Lonicera maackii	1	invasive	invasive	http://www.issg.org/database/species/ecology.asp?si=1225&fr=1&sts=sss&lang=EN
Dias Segura	MSc thesis	2013	None	Lophophora diffusa	1	native	not introduced	restricted
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Lotus arinagensis	1	native	not introduced	restricted

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Kauffman; Maron	Am Nat	2006	10.1086/507877	Lupinus arboreus	2	native	invasive	http://plants.usda.gov/java/invasiveOne?startChar=L
Dangremond; Knight	Ecology	2010	10.1890/09-0418.1	Lupinus tidestromii	3	native	not introduced	restricted
Chien; Zuidema; Nghia	Popul Ecol	2008	10.1007/s10144-008-0079-3	Magnolia fordiana	1	native	not introduced	restricted
Hara; Kanno; Hirabuki; Takehara	J Veg Sci	2004	10.1111/j.1654-1103.2004.tb02286.x	Magnolia salicifolia	1	native	not introduced	restricted
Levine; McEachern; Cowan	J Ecol	2008	10.1111/j.1365-2745.2008.01375.x	Malacothrix indecora	1	native	not introduced	restricted
Contreras; Valverde	J Arid Env	2002	10.1006/jare.2001.0926	Mammillaria crucigera	1	native	not introduced	restricted
Ramos Lopez	MSc thesis	2007	None	Mammillaria dixanthocentron	1	native	not introduced	restricted
Ferrer; Duran; Mendez; Dorantes; Dzib	Bol Soc Bot Mex	2011	None	Mammillaria gaumeri	7	native	not introduced	restricted
Rodriguez Ortega	PhD thesis	2008	None	Mammillaria hernandezii	2	native	not introduced	restricted
Flores Martinez	PhD thesis	2010	None	Mammillaria huitzilopochtli	1	native	not introduced	restricted
Flores-Martinez; Manzanero-Medino; Golubov; Montana; Mandujano	Plant Ecol	2010	10.1007/s11258-010-9737-6	Mammillaria huitzilopochtli	1	native	not introduced	restricted
Valverde; Quijas; Lopez-Villavicencio; Castillo	Plant Ecol	2004	10.1023/B:VEGE.0000021662.78634.de	Mammillaria magnimamma	2	native	not introduced	restricted
Saldivar Sanchez, Navarro Carbajal	Cact Suc Mex	2012	None	Mammillaria mystax	1	native	not introduced	restricted
Rodriguez Ortega	PhD thesis	2008	None	Mammillaria napia	1	native	not introduced	restricted
Valverde; Zavala-Hurtado	J Arid Env	2006	10.1016/j.jaridenv.2005.06.001	Mammillaria pectinifera	1	native	not introduced	restricted
Rodriguez Ortega	PhD thesis	2008	None	Mammillaria solisioides	1	native	not introduced	restricted

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Avendano Calco	MSc thesis	2007	None	Mammillaria supertexta	1	native	not introduced	restricted
Cruz-Rodriguez; Lopez-Villavicencio; Valverde	J Trop Ecol	2009	10.1017/S0266467408005713	Manilkara zapota	1	native	introduced	http://www.hear.org/gcw/species/manilkara_zapota/
Hoffmann	Ecology	1999	10.1890/0012-9658(1999)080[1354:FAPDOW]2.0.CO;2	Miconia albicans	1	native	not introduced	restricted
Pascarella; Alde; Zimmerman	Biotrop	2007	10.1111/j.1744-7429.2006.00220.x	Miconia prasina	2	native	not introduced	restricted
Norghauer; Newbery	Ecol Monog	2011	10.1890/10-2268.1	Microberlinia bisulcata	1	native	not introduced	restricted
Angert	Ecology	2006	10.1890/0012-9658(2006)87[2014:DOCAMP]2.0.CO;2	Mimulus cardinalis	1	native	not introduced	restricted
Angert	Ecology	2006	10.1890/0012-9658(2006)87[2014:DOCAMP]2.0.CO;2	Mimulus lewisii	3	native	introduced	http://www.hear.org/gcw/species/mimulus_lewisii/
Forbis; Doak	Am J Bot	2004	10.3732/ajb.91.7.1147	Minuartia obtusiloba	1	native	not introduced	restricted
Jacquemyn; Brys; Neubert	Ecol Appl	2005	10.1890/04-1762	Molinia caerulea	4	native	introduced	http://www.hear.org/gcw/species/molinia_caerulea/ this paper describes the species as invasive but doesn't specify whether it is the native species or an invasive subsspecies? Please see http://alienplantsbelgium.be/content/molinia-caerulea
Cipriotti; Aguiar	Appl Veg Sci	2012	10.1111/j.1654-109X.2011.01138.x	Mulinum spinosum	1	native	introduced	http://www.hear.org/gcw/species/mulinum_spinosum/
Dostal	J Veg Sci	2007	10.1111/j.1654-1103.2007.tb02519.x	Myosotis ramosissima	5	native	introduced	http://www.hear.org/gcw/species/myosotis_ramosissima/
Hoffmann	Ecology	1999	10.1890/0012-9658(1999)080[1354:FAPDOW]2.0.CO;2	Myrsine guianensis	1	native	not introduced	restricted

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Burns; Pardini; Schutzenhofer; Chung; Seidler; Knight	Ecology	2013	10.1890/12-1310.1	Narcissus poeticus	1	introduced	introduced	https://plants.usda.gov/core/profile?symbol=NAPO
Barkham	J Ecol	1980	10.2307/2259425	Narcissus pseudonarcissus	2	native	invasive	http://www.niiss.org/cwis438/websites/GISINDirectory/GISIN_ScientificName_Info.php?GISIN_ScientificNameID=45839&CallingPage=%2Fcwis438%2Fwebsites%2FGISINDirectory%2FOccurrence_Result.php%3FTakeAction%3DReturned%26ProjectID%3D0%26GISIN_InsertLogID%3D0%26ScientificName%3DNarcissus+pseudonarcissus%26Kingdom%3D0%26Country_AreaID%3D0%26CurrentRow%3D0%26TotalRows%3D-1&CallingLabel=To%20Occurrence%20Search%20Results&WebSiteID=4
Ghimire; Gimenez; Pradel; McKey; Aumeeruddy-Thomas	J Appl Ecol	2008	10.1111/j.1365-2664.2007.01375.x	Nardostachys jatamansi	1	native	not introduced	restricted
Esparza-Olguin; Valverde; Mandujano	Popul Ecol	2005	10.1007/s10144-005-0230-3	Neobuxbaumia macrocephala	1	native	not introduced	restricted
Godinez-Alvarez; Valiente-Banuet	Plant Ecol	2004	10.1023/B:VEGE.0000046052.35390.59	Neobuxbaumia macrocephala	1	native	not introduced	restricted
Esparza-Olguin; Valverde; Mandujano	Popul Ecol	2005	10.1007/s10144-005-0230-3	Neobuxbaumia mezcalaensis	1	native	not introduced	restricted
Arroyo-Cosultchi; Golubov; Mandujano	Acta Oecol	2016	10.1016/j.actao.2016.01.006	Neobuxbaumia polylopha	1	native	not introduced	restricted
Esparza-Olguin; Valverde; Mandujano	Popul Ecol	2005	10.1007/s10144-005-0230-3	Neobuxbaumia tetetzo	1	native	not introduced	restricted
Godinez-Alvarez; Valiente-Banuet	Plant Ecol	2004	10.1023/B:VEGE.0000046052.35390.59	Neobuxbaumia tetetzo	1	native	not introduced	restricted
Godinez Alvarez; Valiente-Banuet; Rojas-Martinez	Ecology	2002	10.1890/0012-9658(2002)083[2617:TROSDI]2.0.CO;2	Neobuxbaumia tetetzo	1	native	not introduced	restricted

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Shefferson; Tali	J Ecol	2007	10.1111/j.1365-2745.2006.01195.x	Neotinea ustulata	5	native	not introduced	restricted
Enright; Ogden	Aust J Ecol	1979	10.1111/j.1442-9993.1979.tb01195.x	Nothofagus fusca	3	native	not introduced	restricted
Thomson	Cons Biol	2005	10.1111/j.1523-1739.2005.004108.x	Oenothera deltoides	1	native	not introduced	restricted
Mandujano; Golubov; Huenneke	Popul Ecol	2007	10.1007/s10144-006-0032-2	Opuntia macrocentra	2	native	not introduced	restricted
Haridas; Keeler; Tenhumberg	Ecology	2015	10.1890/13-1984.1	Opuntia macrorhiza	4	native	not introduced	restricted
Carrillo Angeles	PhD thesis	2011	None	Opuntia microdasys	3	native	invasive	http://www.invasives.org.za/legislation/item/695-bunny-ears-opuntia-microdasys
Mandujano; Montana; Franco; Golubov; Flores-Martinez	Ecology	2001	10.2307/2679864	Opuntia rastrera	2	native	not introduced	restricted
Jacquemyns; Brys; Jongejans	Ecology	2010	10.1890/08-2321.1	Orchis purpurea	6	native	introduced	http://www.hear.org/gcw/species/orchis_purpurea/
Berg	Ecography	2002	10.1034/j.1600-0587.2002.250211.x	Oxalis acetosella	3	native	introduced	http://www.hear.org/gcw/species/oxalis_acetosella/
Chagneau; Mortier; Picard	J R Stat Soc C	2009	10.1111/j.1467-9876.2008.00657.x	Oxandra asbeckii	1	native	not introduced	restricted
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Oxytropis jabalambrensis	2	native	not introduced	restricted
Morales-Romero; Godinez-Alvarez; Campo-Alves; Molino-Freaner	J Arid Env	2012	10.1016/j.jaridenv.2011.09.005	Pachycereus pecten-aboriginum	1	native	not introduced	restricted
Andrieu; Freville; Besnord; Vaudey; Gauthier; Thompson; Debussche	Popul Ecol	2013	10.1007/s10144-012-0346-1	Paeonia officinalis	3	native	introduced	http://eol.org/pages/486255/details
Ishihama; Fujii; Yamamoto; Takada	Popul Ecol	2014	10.1007/S10144-013-0414-1	Paliurus ramosissimus	1	native	not introduced	restricted

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Shahi	PhD thesis	2007	None	Panax quinquefolius	1	native	not introduced	restricted
Van de Voort; McGraw	Biol Cons	2006	10.1016/j.biocon.2006.01.010	Panax quinquefolius	1	native	not introduced	restricted
Nantel; Gagnon; Nault	Cons Biol	1996	10.1046/j.1523-1739.1996.10020608.x	Panax quinquefolius	2	native	not introduced	restricted
Charron; Gagnon	J Ecol	1991	10.2307/2260724	Panax quinquefolius	2	native	not introduced	restricted
Chien; Zuidema; Nghia	Popul Ecol	2008	10.1007/s10144-008-0079-3	Parashorea chinensis	1	native	not introduced	restricted
Raghu; Wilson; Dhileepan	Aust J Ent	2006	10.1111/j.1440-6055.2006.00556.x	Parkinsonia aculeata	1	invasive	invasive	http://www.hear.org/gcw/species/parkinsonia_aculeata/
Iriondo; Albert; Gimenez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Parolinia glabriuscula	1	native	not introduced	restricted
Dalgleish; Koons; Adler	J Ecol	2010	10.1111/j.1365-2745.2009.01585.x	Paronychia jamesii	1	native	not introduced	restricted
Forbis; Doak	Am J Bot	2004	10.3732/ajb.91.7.1147	Paronychia pulvinata	1	native	not introduced	restricted
Menges	Cons Biol	1990	10.1111/j.1523-1739.1990.tb00267.x	Pedicularis furbishiae	1	native	not introduced	restricted
Hartshorn	PhD thesis	1972	None	Pentaclethra macroloba	1	native	not introduced	restricted
Hoffmann; Solbrig	Forest Ecol Manag	2003	10.1016/S0378-1127(02)00566-2	Periandra mediterranea	1	native	not introduced	restricted
McKenna	PhD thesis	2007	None	Persoonia bargoensis	2	native	not introduced	restricted
McKenna	PhD thesis	2007	None	Persoonia glaucescens	2	native	not introduced	restricted
Bradstock; O'Connell	Aust J Bot	1988	10.1111/j.1442-9993.1988.tb00999.x	Petrophile pulchella	1	native	not introduced	restricted
Levine; McEachern; Cowan	J Ecol	2008	10.1111/j.1365-2745.2008.01375.x	Phacelia insularis	1	native	not introduced	restricted

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Ellis; Williams; Lesica; Bell; Bierzychudek; Bowles; Crone; Doak; Ehrlen; Ellis-Adam; McEachern; Ganesan; Latham; Luijten; Kaye; Knight; Menges; Morris; Den Nijs; Oostermeijer; Quintana-Ascencio; Shelly; Stanley; Thorpe; Ticktin; Valverde; Weekley	Ecology	2012	10.1890/11-1052.1	Phyllanthus emblica	1	native	introduced	https://keyserver.lucidcentral.org/weeds/data/media/Html/phyllanthus_emblica.htm
Ticktin; Ganesan; Paramesha; Setty	J Appl Ecol	2012	10.1111/j.1365-2664.2012.02156.x	Phyllanthus emblica	1	native	introduced	https://keyserver.lucidcentral.org/weeds/data/media/Html/phyllanthus_emblica.htm
Ticktin; Ganesan; Paramesha; Setty	J Appl Ecol	2012	10.1111/j.1365-2664.2012.02156.x	Phyllanthus indofischeri	1	native	not introduced	restricted
Dalgleish; Koons; Adler	J Ecol	2010	10.1111/j.1365-2745.2009.01585.x	Physaria ovalifolia	1	native	not introduced	restricted
Bernal	J Appl Ecol	1998	10.1046/j.1365-2664.1998.00280.x	Phytelephas seemannii	1	native	not introduced	restricted
Auestad; Rydgren; Jongejans; Kroon	Biol Cons	2010	10.1016/j.biocon.2009.12.037	Pimpinella saxifraga	3	native	introduced	http://hear.its.hawaii.edu/gcw/species/pimpinella_saxifraga/
Svennson; Carlsson; Karlsson; Nordell	J Ecol	1993	10.2307/2261662	Pinguicula alpina	1	native	not introduced	restricted
Kesler; Trusty; Hermann; Guyer	Oecologia	2008	10.1007/s00442-008-1022-1	Pinguicula ionantha	14	native	not introduced	restricted
Svennson; Carlsson; Karlsson; Nordell	J Ecol	1993	10.2307/2261662	Pinguicula villosa	1	native	not introduced	restricted
Ettl; Cottone.	Book	2004	None	Pinus albicaulis	1	native	not introduced	restricted
van Mantgem; Stephenson	J Ecol	2005	10.1111/j.1365-2745.2005.01007.x	Pinus lambertiana	3	native	introduced	http://www.hear.org/gcw/species/pinus_lambertiana/

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Maloney; Vogler; Eckert; Jensen; Neale	Forest Ecol Manag	2011	10.1016/j.foreco.2011.05.011	Pinus lambertiana	9	native	introduced	http://www.hear.org/gcw/species/pinus_lambertiana/
Buckley; Brockerhoff; Langer; Ledgard; North; Rees	J Appl Ecol	2005	10.1111/j.1365-2664.2005.01100.x	Pinus nigra	2	invasive	invasive	http://www.issg.org/database/species/ecology.asp?si=1817&fr=1&sts=&lang=EN
Platt; Evans; Rathbun	Am Nat	1988	10.1086/284803	Pinus palustris	1	native	introduced	http://www.hear.org/gcw/species/pinus_palustris/
van Mantgem; Stephenson	J Ecol	2005	10.1111/j.1365-2664.2005.01100.x	Pinus ponderosa	1	native	introduced	http://www.hear.org/gcw/species/pinus_ponderosa/
Munzbergova; Hadincova; Wild; Kindlmannova	PLoS ONE	2013	10.1371/journal.pone.0056953	Pinus strobus	1	invasive	invasive	http://www.cabdirect.org/abstracts/20093201602.html;jsessionid=4216A9AFC248075EB8751A2105080D10
Usher	Biom	1966	10.2307/2401258	Pinus sylvestris	1	native	introduced	http://www.hear.org/gcw/species/pinus_sylvestris/
Eriksson; Eriksson	J Veg Sci	2000	10.2307/3236803	Plantago media	2	native	introduced	https://npgsweb.ars-grin.gov/gringlobal/taxonomydetail.aspx?id=400112
Marcante; Winkler; Erschbamer	Annals Bot	2009	10.1093/aob/mcp047	Poa alpina	2	native	introduced	http://www.hear.org/gcw/species/poa_alpina/
Bullock	Biotrop	1980	10.2307/2387694	Podococcus barteri	1	native	not introduced	restricted
Sohn; Policansky	Ecology	1977	10.2307/1935088	Podophyllum peltatum	2	native	introduced	http://www.hear.org/gcw/species/podophyllum_peltatum/
Bermingham	Plant Ecol	2010	10.1007/s11258-010-9762-5	Polemonium van-bruntiae	3	native	introduced	http://eol.org/pages/580849/maps
Maliakal Witt	PhD thesis	2004	None	Polygonella basiramia	2	native	not introduced	restricted
Eriksson	J Ecol	1988	10.2307/2260610	Potentilla anserina	1	native	introduced	https://npgsweb.ars-grin.gov/gringlobal/taxonomydetail.aspx?id=29465
Lesica; Ellis	Invasive Plant Science and Manag	2010	10.1614/IPSM-08-135.1	Potentilla recta	1	invasive	invasive	https://bcinvasives.ca/invasive-species/identify/invasive-plants/sulphur-cinquefoil
Jacquemyn; Brys	Ecology	2008	10.1016/j.biocon.2006.07.016	Primula elatior	7	native	not introduced	restricted
Lindborg; Ehrlen	Cons Biol	2002	10.1046/j.1523-1739.2002.00509.x	Primula farinosa	3	native	not introduced	restricted

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Ehrlen; Syrjinen; Leimu; Garcia; Lehtila	J Appl Ecol	2005	10.1111/j.1365-2664.2005.01015.x	Primula veris	1	native	introduced	http://www.hear.org/gcw/species/primula_veris/
Ehrlen; Syrjinen; Leimu; Garcia; Lehtila	Cons Biol	2006	10.1111/j.1523-1739.2006.00368.x	Primula veris	13	native	introduced	http://www.hear.org/gcw/species/primula_veris/
Endels; Jacquemyn; Brys; Hermy	Plant Ecol	2005	10.1007/s11258-004-0026-0	Primula veris	1	native	introduced	http://www.hear.org/gcw/species/primula_veris/
Valverde; Silvertown	J Ecol	1998	None	Primula vulgaris	8	native	introduced	http://www.hear.org/gcw/species/primula_vulgaris/
Valdes; Garcia; Garcia; Ehrlen	Ecography	2013	10.1111/j.1600-0587.2013.00216.x	Primula vulgaris	14	native	introduced	http://www.hear.org/gcw/species/primula_vulgaris/
Condit	Forest Ecol Manag	1993	10.1016/0378-1127(93)90045-O	Prioria copaifera	1	native	not introduced	restricted
Aschero; Morris; Vazquez; Alvarez; Villagra	For Ecol Manag	2016	10.1016/foreco.2016.03.028	Prosopis flexuosa	1	native	not introduced	restricted
Golubov; Mandujano; Franco; Montana; Eguiarte; Lopez-Portillo	J Ecol	1999	10.1046/j.1365-2745.1999.00420.x	Prosopis glandulosa	1	native	invasive	http://www.issg.org/database/species/ecology.asp?si=137&fr=1&sts=sss&lang=EN
Bernal	PhD thesis	2004	None	Prosopis laevigata	1	native	not introduced	restricted
Stewart	PhD thesis	2001	None	Prunus africana	1	native	not introduced	restricted
Sebert-Cuvillier; Paccaut; Chabrerie; Endels; Goubet; Decoq	Ecol Model	2007	10.1016/j.ecolmodel.2006.09.005	Prunus serotina	1	invasive	invasive	http://www.cabi.org/isc/datasheet/44360
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Pseudomisopates rivas-martinezii	2	native	not introduced	restricted
Vite Gonzalez; Zavala Hurtado	Report	1998	None	Pseudomitrocereus fulviceps	1	native	not introduced	restricted
Duran; Franco	PhD thesis	1992	None	Pseudophoenix sargentii	6	native	not introduced	restricted
Maschinski; Duquesnel	Biol Cons	2006	10.1016/j.biocon.2006.07.012	Pseudophoenix sargentii	1	native	not introduced	restricted

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Somarriba	Agrofor Syst	1988	10.1007/BF02344742	Psidium guajava	1	native	invasive	http://www.issg.org/database/species/ecology.asp?si=211&fr=1&sts=sss&lang=EN
Dalgleish; Koons; Adler	J Ecol	2010	10.1111/j.1365-2745.2009.01585.x	Psoralea tenuiflora	1	native	introduced	http://www.hear.org/gcw/species/psoralea_tenuiflora/
Desmet; Shackleton; Ronbinson	S African J Bot	1996	None	Pterocarpus angolensis	1	native	not introduced	restricted
Mendez; Duran; Olmsted	Biotrop	2004	10.1646/1601	Pterocereus gaumeri	2	native	not introduced	restricted
Liddle; Brook; Matthews; Taylor; Caley	Biol Cons	2006	10.1016/j.biocon.2006.04.028	Ptychosperma macarthurii	1	native	introduced	http://www.hear.org/gcw/species/ptychosperma_macarthurii/
Maschinski; Baggs; Quintana-Ascencio; Menges	Cons Biol	2006	10.1111/j.1523-1739.2006.00272.x	Purshia subintegra	2	native	not introduced	restricted
Pfingsten	PhD thesis	2013	None	Pyrrocoma radiata	4	native	not introduced	restricted
Kaye; Pyke	Ecology	2003	10.1890/0012-9658(2003)084[1464:TEOSTO]2.0.CO;2	Pyrrocoma radiata	5	native	not introduced	restricted
Hiura; Fujiwara	J Veg Sci	1999	10.2307/3237309	Quercus mongolica crispula	1	native	not introduced	restricted
Pico; Riba	Plant Ecol	2002	10.1023/A:1020310609348	Ramonda myconi	5	native	introduced	http://www.hear.org/gcw/species/ramonda_myconi/
Sarukhan; Harper	J Ecol	1973	10.2307/2258643	Ranunculus acris	1	native	invasive	http://www.hear.org/gcw/species/ranunculus_acris/
Sarukhan; Harper	J Ecol	1973	10.2307/2258643	Ranunculus bulbosus	1	native	invasive	http://plants.usda.gov/java/invasiveOne?startChar=R
Idestam-Almquist	PhD thesis	1998	None	Ranunculus peltatus	1	native	not introduced	restricted
Sarukhan; Harper	J Ecol	1973	10.2307/2258643	Ranunculus repens	1	native	invasive	http://www.hear.org/gcw/species/ranunculus_repens/
Dalgleish; Koons; Adler	J Ecol	2010	10.1111/j.1365-2745.2009.01585.x	Ratibida columnifera	1	native	introduced	http://www.hear.org/gcw/species/ratibida_columnifera/
Lopez-Hoffman; Ackerly; Anten; Denoyer;Ramos	J Ecol	2007	10.1111/j.1365-2745.2007.01298.x	Rhizophora mangle	1	native	invasive	http://www.hear.org/pier/species/rhizophora_mangle.htm GISD
McGraw	Am J Bot	1989	10.2307/2444780	Rhododendron maximum	1	native	not introduced	restricted

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Salguero-Gomez	MSc thesis	2004	None	Rhododendron ponticum	8	invasive	invasive	http://www.issg.org/database/species/ecology.asp?si=1651&lang=EN
Travis; Harris; Park; Bullock	MEE	2011	10.1111/j.2041-210X.2011.00104.x	Rhododendron ponticum	1	invasive	invasive	http://www.issg.org/database/species/ecology.asp?si=1651&lang=EN
Enright; Watson	New Zealand J Bot	1992	10.1080/0028825X.1992.10412883	Rhopalostylis sapida	1	native	not introduced	restricted
Nantel; Gagnon	J Ecol	1999	None	Rhus aromatica	4	native	introduced	http://www.hear.org/gcw/species/rhus_aromatica/
Thaxton	PhD thesis	2003	None	Rhus copallinum	1	native	not introduced	restricted
Burns; Pardini; Schutzenhofer; Chung; Seidler; Knight	Ecology	2013	10.1890/12-1310.1	Rosa canina	1	introduced	introduced	https://keyserver.lucidcentral.org/weeds/data/media/Html/rosa_canina.htm
Burns; Pardini; Schutzenhofer; Chung; Seidler; Knight	Ecology	2013	10.1890/12-1310.1	Rosa multiflora	1	invasive	invasive	https://www.cabi.org/isc/datasheet/47824
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Rosmarinus tomentosus	3	native	not introduced	restricted
Hoffmann	Ecology	1999	10.1890/0012-9658(1999)080[1354:FAPDOW]2.0.CO;2	Roupala montana	1	native	not introduced	restricted
Hoffmann	Ecology	1999	10.1890/0012-9658(1999)080[1354:FAPDOW]2.0.CO;2	Rourea induta	1	native	not introduced	restricted
Lambrecht-McDowell; Radosevich	Biol Inv	2005	10.1007/s10530-004-0870-9	Rubus praecox	2	invasive	invasive	http://www.hear.org/gcw/species/rubus_rigidus/
Eriksson	Ecol Research	1994	10.1007/BF02348412	Rubus saxatilis	2	native	not introduced	restricted
Lambrecht-McDowell; Radosevich	Biol Inv	2005	10.1007/s10530-004-0870-9	Rubus ursinus	2	native	not introduced	restricted
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Rumex rupestris	1	native	not introduced	restricted

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Ramp	PhD thesis	1989	None	Sabal minor	1	native	introduced	http://www.hear.org/gcw/species/sabal_minor/
Pulido; Valverde; Caballero	J Trop Ecol	2007	10.1017/S0266467406003877	Sabal yapa	1	native	not introduced	restricted
Tolvanen; Schroderus; Henry	Evol Ecol	2002	10.1007/978-94-017-1345-0_12	Salix arctica	1	native	not introduced	restricted
Abe; Motai; Tanaka; Shibata; Kominami; Nakashizuka	Ecology	2008	10.1890/06-2009.1	Sambucus sieboldiana	15	native	not introduced	restricted
Gustafsson; Ehrlen	Oikos	2003	10.1034/j.1600-0706.2003.11493.x	Sanicula europaea	1	native	not introduced	restricted
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Santolina melidensis	1	native	introduced	http://www.hear.org/gcw/species/sanicula_europaea/
Renne	PhD thesis	2001	None	Sapium sebiferum	5	invasive	introduced	http://www.issg.org/database/species/ecology.asp?si=712&fr=1&sts=sss&lang=EN only classified as invasive in th eUS GISD
Cserg□o; Molnar; Garcia	Popul Ecol	2011	10.1007/s10144-010-0249-y	Saponaria bellidifolia	4	native	introduced	http://www.hear.org/gcw/species/saponaria_bellidifolia/
Salinas; Suarez; Blanca	Can J Bot	2002	10.1139/b02-013	Sarcocapnos baetica	1	native	not introduced	restricted
Salinas; Suarez; Blanca	Can J Bot	2002	10.1139/b02-013	Sarcocapnos enneaphylla	2	native	not introduced	restricted
Salinas; Suarez; Blanca	Can J Bot	2002	10.1139/b02-013	Sarcocapnos pulcherrima	2	native	not introduced	restricted
Ang; de Wreede	Mar Ecol Prog Ser	1990	None	Sargassum siliquosum	1	native	not introduced	restricted
Brewer	Am J Bot	2001	10.2307/3558336	Sarracenia alata	1	native	introduced	http://www.hear.org/gcw/species/sarracenia_alata/
Tendland	MSc thesis	2011	None	Sarracenia purpurea	1	native	invasive	http://www.ipcc.ie/a-to-z-peatlands/peatland-action-plan/invasive-species-on-irish-peatlands/
Gotelli; Ellison	Ecol Appl	2006	10.1890/04-0479	Sarracenia purpurea	2	native	invasive	http://www.ipcc.ie/a-to-z-peatlands/peatland-action-plan/invasive-species-on-irish-peatlands/
Law; Salick; Knight	Plant Ecol	2010	10.1007/s11258-010-9761-6	Saussurea medusa	1	native	not introduced	restricted
Marcante; Winkler; Erschbamer	Annals Bot	2009	10.1093/aob/mcp047	Saxifraga aizoides	2	native	not introduced	restricted
Dinnetz; Nilsson	Plant Ecol	2002	10.1023/A:1015593311183	Saxifraga cotyledon	2	native	not introduced	restricted

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Dostal	J Veg Sci	2007	10.1111/j.1654-1103.2007.tb02519.x	Saxifraga tridactylites	5	native	not introduced	restricted
Verkaar; Schenkeveld	New Phyto	1984	10.1111/j.1469-8137.1984.tb04155.x	Scabiosa columbaria	1	native	introduced	http://www.hear.org/gcw/species/scabiosa_columbaria/
Yamada; Zuidema; Itoh; Yamakura; Okhubo; Kanzaki; Tan; Ashton	J Ecol	2007	10.1111/j.1365-2745.2006.01209.x	Scaphium macropodum	3	native	not introduced	restricted
Munzbergova	Folia Geobot	2006	10.1007/bf02806475	Scorzonera hispanica	1	native	introduced	http://www.hear.org/gcw/species/scorzonera_hispanica/
Cipriotti; Aguiar	Appl Veg Sci	2012	10.1111/j.1654-109X.2011.01138.x	Senecio filaginoides	1	native	introduced	http://www.hear.org/gcw/species/senecio_filaginoides/
Namkoong; Roberds	Am Nat	1974	10.1086/282913	Sequoia sempervirens	1	NATD	NATD	http://www.hear.org/gcw/species/sequoia_sempervirens/
Yamada; Yamada; Okuda; Fletcher	Oecologia	2013	10.1007/s00442-012-2529-z	Shorea acuminata	3	native	not introduced	restricted
Yamada; Yamada; Okuda; Fletcher	Oecologia	2013	10.1007/s00442-012-2529-z	Shorea bracteolata	3	native	not introduced	restricted
Yamada; Yamada; Okuda; Fletcher	Oecologia	2013	10.1007/s00442-012-2529-z	Shorea leprosula	3	native	not introduced	restricted
Visser; Jongejans; van Breugel; Zuidema; Chen; Kassim; de Kroon	J Ecol	2011	10.1111/j.1365-2745.2011.01825.x	Shorea leprosula	1	native	not introduced	restricted
Yamada; Yamada; Okuda; Fletcher	Oecologia	2013	10.1007/s00442-012-2529-z	Shorea maxwelliana	3	native	not introduced	restricted
Yamada; Yamada; Okuda; Fletcher	Oecologia	2013	10.1007/s00442-012-2529-z	Shorea ovalis	3	native	not introduced	restricted
Morris; Doak	Am J Bot	1998	None	Silene acaulis	5	native	introduced	http://www.hear.org/gcw/species/silene_acaulis/
Kephart; Paladino	Am J Bot	1997	10.2307/2446079	Silene douglasii oraria	2	native	not introduced	restricted
Garcia; Guzman; Goni	Biol Cons	2002	10.1016/S0006-3207(01)00113-6	Silene glaucifolia pseudoviscosa	3	native	not introduced	restricted

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Menges; Dolan	J Ecol	1998	10.1046/j.1365-2745.1998.00234.x	Silene regia	1	native	not introduced	restricted
Lesica; Crone	J Ecol	2007	10.1111/j.1365-2745.2007.01291.x	Silene spaldingii	1	native	not introduced	restricted
Schmid	JPDP	1990	None	Solidago altissima	1	NATD	NATD	
Dalgleish; Koons; Adler	J Ecol	2010	10.1111/j.1365-2745.2009.01585.x	Solidago mollis	1	native	not introduced	restricted
Silva; Mejias; Garcia	Bas Appl Ecol	2015	10.1016/j.baae.2015.02.009	Sonchus pustulatus	1	native	not introduced	restricted
Dalgleish; Koons; Adler	J Ecol	2010	10.1111/j.1365-2745.2009.01585.x	Sphaeralcea coccinea	1	native	introduced	http://www.hear.org/gcw/species/sphaeralcea_coccinea/
Dalgleish; Kula; Hartnett; Sandercook	Am J Bot	2008	10.3732/ajb.2007277	Sporobolus heterolepis	1	native	introduced	http://www.hear.org/gcw/species/sporobolus_heterolepis/
Dalgleish; Koons; Adler	J Ecol	2010	10.1111/j.1365-2745.2009.01585.x	Stenaria nigricans	1	native	not introduced	restricted
Clark-Tapia	PhD thesis	2004	None	Stenocereus eruca	2	native	not introduced	restricted
Guardia; Raventos; Caswell	J Ecol	2000	10.1046/j.1365-2745.2000.00504.x	Stipa calamagrostis	2	native	introduced	http://www.hear.org/gcw/species/achnatherum_calamagrostis/
Hartshorn	PhD thesis	1972	None	Stryphnodendron microstachyum	1	native	not introduced	restricted
Abe; Nokashizuka; Tanoka	J Veg Sci	1998	10.2307/3237044	Styrax obassia	9	native	not introduced	restricted
Milden	PhD thesis	2005	None	Succisa pratensis	3	native	introduced	http://www.hear.org/gcw/species/succisa_pratensis/
Jongejans; de Kroon	J Ecol	2005	10.1111/j.1365-2745.2005.01003.x	Succisa pratensis	5	native	introduced	http://www.hear.org/gcw/species/succisa_pratensis/
Wallin; Svensson	Folia Geobot	2012	10.1007/s12224-012-9123-3	Succisa pratensis	3	native	introduced	http://www.hear.org/gcw/species/succisa_pratensis/

Authors	Journal	Year	DOI_ISBN	Species	Number of populations	Population Status	Species Status	Species Status Source
Pavlik; Barbour	Biol Cons	1988	10.1016/0006-3207(88)90069-9	Swallenia alexandrae	1	native	not introduced	restricted
Verwer; Pena-Claros; van der Staak; Ohlson-Kiehn; Sterck	J Appl Ecol	2008	10.1111/j.1365-2664.2008.01564.x	Swietenia macrophylla	1	native	invasive	http://www.hear.org/pier/species/swietenia_macrophylla.htm
Schmidt; Ticktin	Biol Cons	2012	10.1016/j.biocon.2012.03.018	Syngonanthus nitens	8	native	not introduced	restricted
Brown; Spector; Wu	J Appl Ecol	2008	10.1111/j.1365-2664.2008.01550.x	Syzygium jambos	1	invasive	invasive	http://www.issg.org/database/species/ecology.asp?si=920&fr=1&sts=sss&lang=EN GISD
Burns; Pardini; Schutzenhofer; Chung; Seidler; Knight	Ecology	2013	10.1890/12-1310.1	Taraxacum campylodes	1	introduced	invasive	http://www.issg.org/database/species/ecology.asp?si=427&fr=1&sts=sss&lang=EN plants.usda.gov
Kwit; Horvitz; Platt	Cons Biol	2004	10.1111/j.1523-1739.2004.00567.x	Taxus floridana	3	native	introduced	http://www.hear.org/gcw/species/taxus_floridana/
Norghauer; Newbery	Ecol Monog	2011	10.1890/10-2268.1	Tetraberlinia bifoliolata	1	native	not introduced	restricted
Campbell; Husband	Heredity	2005	10.1038/sj.hdy.6800653	Tetraneuris herbacea	2	native	not introduced	restricted
Dalgleish; Koons; Adler	J Ecol	2010	10.1111/j.1365-2745.2009.01585.x	Thelesperma megapotamicum	1	native	not introduced	restricted
O'Connor; Pickett	J Appl Ecol	1992	10.2307/2404276	Themeda triandra	2	native	introduced	http://www.hear.org/gcw/species/themeda_triandra/
Olmsted; Alvarez-Buylla	Ecol Appl	1995	10.2307/1942038	Thrinax radiata	4	native	not introduced	restricted
Garcia	Ecosistemas	2007	None	Thymus loscosii	1	native	not introduced	restricted
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Thymus vulgaris	1	native	introduced	http://www.hear.org/gcw/species/thymus_vulgaris/ eol
Mondragon; Duran; Ramirez; Valverde	J Trop Ecol	2004	10.1017/S0266467403001287	Tillandsia brachycaulos	1	native	not introduced	restricted
Winkler; Hulber; Hietz	Bas and Appl Ecol	2007	10.1016/j.baae.2006.05.003	Tillandsia deppeana	1	native	not introduced	restricted
Winkler; Hulber; Hietz	Bas and Appl Ecol	2007	10.1016/j.baae.2006.05.003	Tillandsia juncea	1	native	not introduced	restricted

Authors	Journal	Year	DOI_ISBN	Species	Number of populations	Population Status	Species Status	Species Status Source
Mondragon; Ticktin	Cons Biol	2011	10.1111/j.1523-1739.2011.01691.x	Tillandsia macdougallii	1	native	not introduced	restricted
Winkler; Hulber; Hietz	Bas and Appl Ecol	2007	10.1016/j.baae.2006.05.003	Tillandsia multicaulis	1	native	not introduced	restricted
Toledo-Aceves; Hernandez-Apolinar; Valverde	Acta Oeco	2014	10.1016/j.actao.2014.05.009	Tillandsia multicaulis	1	native	not introduced	restricted
Toledo-Aceves; Hernandez-Apolinar; Valverde	Acta Oeco	2014	10.1016/j.actao.2014.05.009	Tillandsia punctulata	1	native	not introduced	restricted
Valverde; Bernal	Bol Soc Bot Mex	2010	0366-2128	Tillandsia recurvata	8	native	not introduced	restricted
Mondragon; Ticktin	Cons Biol	2011	None	Tillandsia violacea	1	native	not introduced	restricted
Calvo	Ecology	1993	10.2307/1940473	Tolumnia variegata	1	native	not introduced	restricted
Schwartz; Hermann; Mantgem	Cons Biol	2000	10.1046/j.1523-1739.2000.98393.x	Torreya taxifolia	1	native	not introduced	restricted
Ohara; Takada; Kawano	Plant Spp Biol	2001	10.1046/j.1442-1984.2001.00062.x	Trillium apetalon	1	native	not introduced	restricted
Ohara; Tomimatsu; Takada; Kawano	Plant Spp Biol	2006	10.1111/j.1442-1984.2006.00145.x	Trillium camschatcense	1	native	not introduced	restricted
Knight	Am J Bot	2003	10.3732/ajb.90.8.1207	Trillium grandiflorum	12	native	not introduced	restricted
Schmucki	PhD thesis	2009	10.1007/sl 1258-008-9460-8	Trillium grandiflorum	10	native	not introduced	restricted
Ream	PhD thesis	2011	None	Trillium ovatum	1	native	not introduced	restricted
Plank	MSc thesis	2010	None	Trillium persistens	4	native	not introduced	restricted
Scanga; Leopold	Biol Cons	2012	10.1016/j.biocon.2012.01.061	Trollius laxus	1	native	not introduced	restricted
Scanga	Plant Ecol	2014	10.1007/s11258-014-0344-9	Trollius laxus	6	native	not introduced	restricted
Lamar; McGraw	Forest Ecol Manag	2005	10.1016/j.foreco.2005.02.056	Tsuga canadensis	1	native	introduced	Johnson O. & More D. (2004)ÊTree Guide: The Most Complete Field Guide to the Trees of Britain and Europe. Collins

Authors	Journal	Year	DOI_ISBN	Species	Number of populations	Population Status	Species Status	Species Status Source
Hu; Wang	Acta Ecol Sinica	1988	None	Vatica mangachapoi	1	native	not introduced	restricted
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Vella pseudocytisus	2	native	not introduced	restricted
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Vella pseudocytisus paui	2	native	not introduced	restricted
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Verbascum fontqueri	3	native	not introduced	restricted
Dostal	J Veg Sci	2007	10.1658/1100-9233(2007)18[91:PDOAIP]2.0.CO;2	Veronica arvensis	1	native	not introduced	restricted
Dostal	J Veg Sci	2007	10.1658/1100-9233(2007)18[91:PDOAIP]2.0.CO;2	Veronica arvensis	4	native	not introduced	restricted
Burns; Pardini; Schutzenhofer; Chung; Seidler; Knight	Ecology	2013	10.1890/12-1310.1	Veronica arvensis	1	native	not introduced	restricted
Yates; Ladd; Coates; McArthur	Aust J Bot	2007	10.1071/BT06032	Verticosa staminosa staminosa	1	native	not introduced	restricted
Hara; Kanno; Hirabuki; Takehara	J Veg Sci	2004	10.1111/j.1654-1103.2004.tb02286.x	Viburnum furcatum	1	native	not introduced	restricted
Eckstein; Otte	Flora	2004	10.1078/0367-2530-00151	Viola elatior	2	native	not introduced	restricted
Eckstein; Danihelka; Otte	Biol	2009	10.2478/s11756-009-0002-1	Viola persicifolia	2	native	not introduced	restricted
Eckstein; Danihelka; Otte	Biol	2009	10.2478/s11756-009-0002-1	Viola pumila	2	native	not introduced	restricted
Solbrig; Sarandon; Bossert	Am Nat	1988	10.1086/284796	Viola sagittata ovata	1	native	not introduced	restricted
Iriondo; Albert; Giminez; Lozano; Escudero	Book	2009	978-84-8014-746-0	Vitaliana primuliflora	1	native	not introduced	restricted

Authors	Journal	Year	DOI_ISBN	Species	Number of populations	Population Status	Species Status	Species Status Source
Chagneau; Mortier; Picard	J R Stat Soc C	2009	10.1111/j.1467-9876.2008.00657.x	Vouacapoua americana	1	native	not introduced	restricted
Zotz	Acta Oeco	2005	10.1016/j.actao.2005.05.009	Vriesea sanguinolenta	3	native	not introduced	restricted
Shriver; Cutler; Doak	Oecologia	2012	10.1007/s00442-012-2301-4	Vulpicida pinastri	1	native	not introduced	restricted
Sanchez-Velazquez; Ezcurra; Martinez-Ramos; Alvarez-Buylla; Lorente	J Ecol	2002	10.1046/j.1365-2745.2002.00702.x	Zea diploperennis	1	native	not introduced	restricted

2. Supplementary Material SM2: Methodological Notes

Robustness of Statistical Analyses

We chose to describe our analyses of demographic metrics (stable population growth, demographic inertia) using Monte Carlo Markov Chain generalised linear mixed models, because of the special features of our dataset. In our raw data, we have demographic indices for each population of each species in each year of measurement. These indices measure population dynamics, which project forward in time. To prevent conflation of time-dependent data and time-dependent metrics, we summarised each population's demography using a time-averaged population projection matrix (PPM). This yielded replicate population-level PPMs for each species. We needed a statistical modelling tool which can tease apart the phylogenetic non-independence of the data (species-level shared evolutionary history); repeated measures per species (multiple populations) and the fact that each species could contribute populations to more than one "population status" category (for example Carduus nutans, an invasive species, has been measured in both its native and its introduced ranges). MCMCglmm is the best statistical algorithm, to our knowledge, that achieves valid analysis of this hierarchical design.

However, we recognise that a full analysis of demographic metrics measured at the population scale, with multiple populations per species, which themselves are patterned phylogenetically, is a weighty analysis that can be hard to explain in a restricted word count and for a wide readership. Also, an analysis that uses population as its experimental unit means that predictions must be made for populations, not for species. Hence we chose to report a simplified analysis that derived mean demographic metrics per species. This approach still required MCMCglmm because a small number of species were represented across multiple "population status" categories. The results of this "per species per status" analysis are presented in the manuscript. To check the robustness of the results, we performed the full-scale "per population per species" analysis and found patterns that matched the results presented (Supplementary Material SM4; Fig.SM1). We also down-scaled the analyses presented here, first by removing species that were represented in multiple "population status" categories. This allowed us to use a generalised least squares regression model with phylogenetic correlation structure (PGLS) because each species was represented just once in the simplified dataset. The significance of the differences between categories, for each demographic metric, were the same as presented in the manuscript (Supplementary Materials SM4). Throughout all the checks of alternative models, the same pattern of results emerged: stable population growth rates were highest (and significantly so) among species measured in the naturalised range, irrespective of their invasiveness. Meanwhile demographic inertia, describing the ability of populations to recover following disturbance, was highest (and significantly so) for invasive species, even when measured in their native range.

3. R code to replicate the analyses in the paper

2.1 Set up

Load required R packages

```
library(popdemo)
library(popbio)
library(MCMCglmm)
library(ape)
library(nlme)
```

Read in data

- the adapted COMPADRE dataset

- the COMPADRE phylogeny

(*after setting the directory/path*)

```
direc<-"C:/Users/mjs245/Dropbox/Plant Invasiveness 
paper/Rmarkdownfinal/"
compadre_full<-read.csv(paste0(direc,"COMPADRE filtered Jelbert 
et al.csv"), header=T)
tree<-read.tree(paste0(direc,"phylogeny_test.tre"))
```

Define required functions:

Function to convert post-reproductive census projection matrix models to pre-reproductive census models.

In post-reproductive models, the recruitment row describes a "seed" or "propagule" stage that is contributed into by reproductive adults, which have survived for the preceding projection interval. To convert to pre-reproductive census, which is the more prevalent representation, recruitment rates are divided by their respective adult rates of survival and growth; then multiplied by rates of germination, survival and growth of propagules, and added to the relevant rows and columns of the converted projection matrix.

```
convert2pre <- function(mat,matF,matC,problem)
{
  if(problem=="pre"){mat_corrected_pre<-mat}else{
    mat <- Matlab2R(mat)
    matF <- Matlab2R(matF)
    matC <- Matlab2R(matC)
    matS<-mat-matF-matC
    matrix_size <- nrow(mat)
    if(problem=="error"){
      newmat<-matS%*%matF+matC+matS
    }
    if (problem=="post"){ # persistent seedbank
      surv_vec<-apply(matS,2,sum)
      surv_mat<-
matrix(surv_vec,nrow=matrix_size,ncol=matrix_size,byrow=T)
      newmat1<-matF/surv_mat
      newmat<-matS%*%newmat1+matC+matS
    }
    if(mat[1,1]==0){
      mat_corrected_pre<-
newmat[2:matrix_size,2:matrix_size]}else{
        mat_corrected_pre<-newmat}

    mat_corrected_pre<- R2Matlab(mat_corrected_pre)
  }
  return(mat_corrected_pre)
}
```

2.2 R code for conversion of projection matrix models to standardise analyse

Code uses the full PPM (mat), the Fecundity part of the PPM (matF), and the clonal reproduction part of the PPM (matC), extracted from the COMPADRE database. Code consists of functions that (a) deal with the “seeds error”, in which fecundity is falsely recorded as a full-year life cycle transition; and (b) converts post-reproductive census projection matrix models to pre-reproductive census models. (a) This function multiplies seed production by rates of seed survival, germination and growth, to better represent recruitment as the full-year life cycle transition. The outcome tends to reduce matrix dimension by a single life stage (removing the false “seed” stage). (b) In post-reproductive models, the recruitment row describes a “seed” or “propagule” stage that is contributed into by reproductive adults, which have survived for the preceding projection interval. To convert to pre-reproductive census, which is the more prevalent representation, recruitment rates are divided by their respective adult rates of survival and growth; then multiplied by rates of germination, survival and growth of propagules, and added to the relevant rows and columns of the converted projection matrix.

Convert to pre-reproductive matrices from post-reproductive matrices and from those with error in the propagule stage

```
PPM<-as.character(compadre_full$matrix_a_string)
PPMfix<-PPM
F<-as.character(compadre_full$matrix_f_string)
C<-as.character(compadre_full$matrix_c_string)
pp<-compadre_full$fixed_census_timing
for(i in 1:dim(compadre_full)[1]){

if(compadre_full$fixed_census_timing[i]%in%c("error","post")){PP
Mfix[i]<-try(convert2pre(PPM[i],F[i],C[i],pp[i]))}
}
compadre_full$Afix<-PPMfix
compadre<-compadre_full
```

Subset rows of dataframe to remove seasonal and laboratory matrices

```
compadre<-compadre[(!compadre$matrix_composition=="NDY -
Seasonal" & !compadre$population_ecoregion=="LAB"),]
compadre<-compadre[(!compadre$matrix_treatment_type.1=="LAB"),]
```

Remove any rows with population_name that includes a semicolon

This means that:

- only keep individual matrices for populations with multiple matrices
- keep the mean matrix for those populations with only one matrix

```
compadre<-compadre[-
grep(";",compadre$population_name,value=FALSE),]
```

(optional) Retain only unmanipulated treatment types

```
compadre<-
compadre[compadre$matrix_treatment_type=="Unmanipulated",]
```

Create list of mean matrices for each population (2965 in total)

```
PPM<-as.character(compadre$Afix)
PPMs<-as.list(numeric(length(PPM)))
Dimensions<-numeric(length(PPM))
Sp<-as.character(compadre$species_accepted)
Pop<-as.character(compadre$population_name)
for(i in 1:length(PPMs)){
  PPMs[[i]]<-Matlab2R(PPM[i])
  Dimensions[i]<-dim(PPMs[[i]])[1]
}
```

2.3 R code for the handling of the filtered COMPADRE dataset containing population projection matrices

Including information on taxonomy, invasive status, population, year and other ancillary information. Seasonal projection matrices and any “populations” measured in a laboratory setting have previously been filtered out. Populations experiencing experimental treatments have also already been filtered out. Aggregate PPMs, formed from individual population replicates, have also been pre-excluded. This section of code creates a mean matrix through time for each population and then filters out any reducible, imprimitive and non-ergodic matrices. The outcome is a dataset, with one row per population, that includes the mean matrix (averaged through time), and all associated taxonomic and status metadata.

The subsequent section of code aggregates dataframe information on species, matrix dimensions and location to add to the dataframe.

First combine species with same dimensions and in same population location to create a unique id for each array.

1. paste population site following species ID

2. paste dimension to ensure similar dimensions are compared across similar species

3. group to unique levels

```
Sp3<-paste(Sp,Pop,sep=".")
Sp3<-paste(Sp3,as.character(Dimensions),sep=".x")
Sp3<-as.factor(noquote(Sp3))
ID<-levels(Sp3)
```

Then create a list of arrays of replicated matrices:

- First create empty lists/vectors

```
aggrPPMs<-as.list(numeric(length(ID)))
reps<-numeric(length(ID))
orders<-numeric(length(ID))
for(i in 1:length(ID)){
  orders[i]<-mean(Dimensions[Sp3==ID[i]])
  reps[i]<-length(which(Sp3==ID[i]))
  aggrPPMs[[i]]<-numeric(orders[i]^2*reps[i])
  dim(aggrPPMs[[i]])<-c(orders[i],orders[i],reps[i])
}
```

- Then add aggregate matrices across duplicated matrices for each population for each species

```
for(i in 1:length(ID) ){
  for(j in 1:reps[i]){
    aggrPPMs[[i]][,,j]<-PPMs[Sp3==ID[i]][[j]]
  }}
```

Now merge meta-data with new aggregated matrices

```
spa<-paste(unique(Sp))
Species<-factor(length(ID),levels=c(spa))

ss<-paste(unique(compadre$population_invasive_status_study))
Status<-factor(length(ID),levels=c(ss))

se<-paste(unique(compadre$population_invasive_status_elsewhere))
Status.Else<-factor(length(ID),levels=c(se))

po<-paste(unique(compadre$taxonomy_order))
plant.order<-factor(length(ID),levels=c(po))

Year<-numeric(length(ID))
```

Create new empty fields/columns ready to store information in a reduced dataframe

Then fill these columns from the original dataframe

1. matrix treatment type

```
mtrt<-paste(unique(compadre$matrix_treatment_type))
matrix_treatment<-factor(length(ID),levels=c(mtrt))

for(i in 1:length(ID)){
  Species[i]<-(Sp[Sp3==ID[i]][1])
  Year[i]<-compadre$publication_year[Sp3==ID[i]][1]
  Status[i]<-
compadre$population_invasive_status_study[Sp3==ID[i]][1]
  Status.Else[i]<-
compadre$population_invasive_status_elsewhere[Sp3==ID[i]][1]
  plant.order[i]<-compadre$taxonomy_order[Sp3==ID[i]][1]
```

```
  matrix_treatment[i]<-
compadre$matrix_treatment_type[Sp3==ID[i]][1]
}
```

This section of code removes some incorrect matrices from the analysis (NA/non-ergodic/non-irreducible/non-primitive)

```
mean.A<-vector("list", length(ID))
check.A<-numeric(length(ID))
for(i in 1:length(ID)){
  mean.A[[i]]<-apply(aggrPPMs[[i]],c(1,2),mean,na.rm=T)
  check.A[i]<-sum(mean.A[[i]])
}
mean.A<-mean.A[!is.na(check.A)]
ID<-ID[!is.na(check.A)]
check.matrices<-mean.A

erg<-factor(length(check.matrices),levels=c("TRUE","FALSE"))
irreducible<-
factor(length(check.matrices),levels=c("TRUE","FALSE"))
primitivity<-
factor(length(check.matrices),levels=c("TRUE","FALSE"))

for (i in 1:length(mean.A)){
  erg[i]<-is.matrix_ergodic(mean.A[[i]])
  irreducible[i]<-is.matrix_irreducible(mean.A[[i]])
  primitivity[i]<-is.matrix_primitive(mean.A[[i]])
}

delete<-which(erg=="FALSE")
delete1<-which(irreducible=="FALSE")
delete2<-which(primitivity=="FALSE")
del<-unique(c(delete,delete1,delete2))

mean.A<-mean.A[-del]
ID.check<-ID[-del]
A.string<-character(length(ID.check))
for(i in 1:length(ID.check)){
  A.string[i]<-R2Matlab(mean.A[[i]])}
```

We can now create multi_pop dataframe using the new variables and information from which matrices passed checks in the previous section of code

We also generate empty vectors to store the demographic response variables and then populate them

```
multi_pop<-
data.frame(Species,Status,Status.Else,Year,plant.order,matrix_tr
eatment)
multi_pop<-multi_pop[!is.na(check.A),]
```

```
multi_pop<-multi_pop[-del,]
multi_pop$ID.check<-ID.check

multi_pop$lambda.mean<-numeric(dim(multi_pop)[1])
multi_pop$inertiaup.mean<-numeric(dim(multi_pop)[1])
multi_pop$inertiadown.mean<-numeric(dim(multi_pop)[1])
multi_pop$reactivity.mean<-numeric(dim(multi_pop)[1])
multi_pop$maxatt.mean<-numeric(dim(multi_pop)[1])
multi_pop$maxamp.mean<-numeric(dim(multi_pop)[1])

for(i in 1:dim(multi_pop)[1]){
  multi_pop$lambda.mean[i]<-abs(eigen(mean.A[[i]])$values[1])
  multi_pop$inertiaup.mean[i]<-
inertia(mean.A[[i]],bound="upper")
  multi_pop$inertiadown.mean[i]<-
inertia(mean.A[[i]],bound="lower")
  multi_pop$reactivity.mean[i]<-reactivity(mean.A[[i]])
  multi_pop$maxatt.mean[i]<-maxatt(mean.A[[i]])
  multi_pop$maxamp.mean[i]<-maxamp(mean.A[[i]])
}
multi_pop$A<-A.string
```

2.4 R code to add phylogenetic data and prepare final dataframes for analysis

Data handling code to match phylogeny to per-species demographic indices, eventually producing the results offered in the main text. This code matches the species names in the dataset containing mean demographic indices per population with species names in the phylogeny. Mismatches are dealt with case-by-case, usually by removing subspecies status from the COMPADRE dataset. The code then calculates mean demographic indices (stable population growth, maximum amplification and minimum attenuation) for each species. Code calculates species' invasive status (restricted vs naturalised non-invasive vs invasive) and population status (native range vs naturalised range). This is not a factorial analysis because there are no representative species in the "restricted, measured in the naturalised range category" (such populations cannot exist).

Rename any subspecies in the multi_pop dataset so that they can be found in the phylogeny

```
multi_pop$species_tree<-gsub(" ", "_", multi_pop$Species)
multi_pop$species_tree<-gsub("Adenocarpus_aureus_gibbsianus",
"Adenocarpus_aureus", multi_pop$species_tree)
multi_pop$species_tree<-gsub("Adenocarpus_gibbsianus",
"Adenocarpus_aureus", multi_pop$species_tree)
multi_pop$species_tree<-gsub("Anthyllis_vulneraria_alpicola",
"Anthyllis_vulneraria", multi_pop$species_tree)
multi_pop$species_tree<-
```

```
gsub("Anthyllis_vulneraria_subsp_alpicola",
"Anthyllis_vulneraria", multi_pop$species_tree)
multi_pop$species_tree<-gsub("Antirrhinum_molle_lopesianum",
"Antirrhinum_molle", multi_pop$species_tree)
multi_pop$species_tree<-gsub("Arenaria_grandiflora_bolosii",
"Arenaria_grandiflora", multi_pop$species_tree)
multi_pop$species_tree<-gsub("Chamaecrista_lineata_keyensis",
"Chamaecrista_lineata", multi_pop$species_tree)
multi_pop$species_tree<-gsub("Betula_pubescens_pumila",
"Betula_pubescens", multi_pop$species_tree)
multi_pop$species_tree<-gsub("Dodonaea_viscosa_angustifolia",
"Dodonaea_viscosa", multi_pop$species_tree)
multi_pop$species_tree<-gsub("Echinospartum_ibericum_algibicum",
"Echinospartum_ibericum", multi_pop$species_tree)
multi_pop$species_tree<-
gsub("Eriogonum_longifolium_gnaphalifolium",
"Eriogonum_longifolium", multi_pop$species_tree)
multi_pop$species_tree<-gsub("Chamaecrista_lineata_keyensis",
"Chamaecrista_lineata", multi_pop$species_tree)
multi_pop$species_tree<-gsub("Gaura_neomexicana_coloradensis",
"Gaura_neomexicana", multi_pop$species_tree)
multi_pop$species_tree<-gsub("Geonoma_pohliana_weddelliana",
"Geonoma_pohliana", multi_pop$species_tree)
multi_pop$species_tree<-gsub("Gilia_tenuiflora_hoffmannii",
"Gilia_tenuiflora", multi_pop$species_tree)
multi_pop$species_tree<-gsub("Leontopodium_nivale_alpinum",
"Leontopodium_nivale", multi_pop$species_tree)
multi_pop$species_tree<-gsub("Lespedeza_juncea_sericea",
"Lespedeza_juncea", multi_pop$species_tree)
multi_pop$species_tree<-gsub("Magnolia_macrophylla_dealbata",
"Magnolia_macrophylla", multi_pop$species_tree)
multi_pop$species_tree<-gsub("Pityopsis_aspera_aspera",
"Pityopsis_aspera", multi_pop$species_tree)
multi_pop$species_tree<-gsub("Quercus_mongolica_crispula",
"Quercus_mongolica", multi_pop$species_tree)
multi_pop$species_tree<-gsub("Silene_douglasii_oraria",
"Silene_douglasii", multi_pop$species_tree)
multi_pop$species_tree<-gsub("Silene_glaucifolia_pseudoviscosa",
"Silene_glaucifolia", multi_pop$species_tree)
multi_pop$species_tree<-
gsub("Tragopogon_pratensis_subsp._Orientalis",
"Tragopogon_pratensis", multi_pop$species_tree)
multi_pop$species_tree<-
gsub("Tragopogon_pratensis_subsp._Pratensis",
"Tragopogon_pratensis", multi_pop$species_tree)
multi_pop$species_tree<-gsub("Vella_pseudocytisus_paui",
"Vella_pseudocytisus", multi_pop$species_tree)
multi_pop$species_tree<-gsub("Verticosa_staminosa_staminosa",
"Verticosa_staminosa", multi_pop$species_tree)
multi_pop$species_tree<-gsub("Viola_sagittata_ovata",
"Viola_sagittata", multi_pop$species_tree)
multi_pop$species_tree<-gsub("Alnus_incana_rugosa",
"Alnus_incana", multi_pop$species_tree)
multi_pop$species_tree<-gsub("Escobaria_robbinsiorum",
"Escobaria_robbinsorum", multi_pop$species_tree)
multi_pop$species_tree<-gsub("Mammillaria_napia",
"Mammillaria_napina", multi_pop$species_tree)
multi_pop$species_tree<-gsub("Styrax_obassia", "Styrax_obassis",
```

```
multi_pop$species_tree)
multi_pop$species_tree<-gsub("Verticosa_staminosa",
"Verticordia_staminosa", multi_pop$species_tree)
```

Check phylogeny for species and create missing vector to store information on which species lack phylogenetic data (now subspecies have been renamed)

```
species_check<-unique(multi_pop$Species)
multi_pop$species_tree<-gsub(" ", "_", multi_pop$Species)
species_tree<-unique(tree$tip.label)
species_data<-unique(multi_pop$species_tree)
missing<-setdiff(species_data,species_tree)
```

Remove any rows of the multi_pop dataframe that don't have phylogenetic information. Create animal column/field that contains link to phylogenetic information within MCMCglmmm models

```
multi_pop_phylo<-
multi_pop[multi_pop$species_tree%in%tree$tip.label,]
multi_pop_phylo$animal<-multi_pop_phylo$species_tree
```

Trim phylogeny to only retain species in the new multi_pop dataframe

```
compadre.incpos<-which(tree$tip.label %in%
multi_pop_phylo$animal)
compadre.exclude<-tree$tip.label[-compadre.incpos]
compadre.tree<-drop.tip(tree,compadre.exclude)
```

Remove internal node labels from the phylogeny, leaving only tip labels

```
compadre.tree$node.label<-NULL
```

Create final "invas" dataframe for analysis

- Create plant.was and plant.is columns to store information on population "status"
- Create log-transformed versions of the response variables
- Create Invasive Category explanatory variable

1. Native

2. Introduced, native range

3. Introduced, non-native range

4. Invasive, native range

5. Invasive, non-native range

```
invas<-multi_pop_phylo
invas$plant.was<-rep("nonnative",dim(invas)[1])
invas$plant.was[invas$Status=="native"]<-"native"
invas$plant.was<-factor(invas$plant.was)
invas$Status.Else[invas$Status.Else=="not
introduced"&invas$Status=="introduced"]<-"introduced"
invas$plant.is<-factor(invas$Status.Else)
levels(invas$plant.is)
invas$plant.is[invas$plant.is=="Introduced"]<-"introduced"
invas$plant.is[invas$plant.is=="Not introduced"]<-"not
introduced"
invas$plant.is[invas$plant.is=="NATD"]<-NA
invas$plant.is<-factor(invas$plant.is)
levels(invas$plant.is)
levels(invas$plant.was)
invas<-invas[!is.na(invas$plant.is),]

invas$loglambda<-log(invas$lambda.mean)
invas$loginertiaup<-log(invas$inertiaup.mean)
invas$loginertiadown<-log(invas$inertiadown.mean)
invas$logmaxatt<-log(invas$maxatt.mean)
invas$logmaxamp<-log(invas$maxamp.mean)
invas$logreac<-log(invas$reactivity.mean)

invas$invasive.category<-
factor(1+(invas$plant.is%in%c("introduced","Introduced"))+(invas
$plant.was=="nonnative")+3*(invas$plant.is=="invasive"))
```

Some slight ammednments to invas dataframe

- Create column containing information on matrix dimensions
- only include “Unmanipulated” populations/matrices
- Remove Miscanthus giganteus
- Make Invasive Category a factor

```
invas$n<-numeric(dim(invas)[1])
for(i in 1:dim(invas)[1]){
  A<-as.matrix(Matlab2R(as.character(invas$A[i])))
  invas$n[i]<-dim(A)[1]
}
invas<-invas[invas$matrix_treatment=="Unmanipulated",]
invas$invasive.category<-factor(invas$invasive.category)
```

Create persp dataframe

This dataframe contains only a mean of each response variable per species (rather than having multiple populations per species) and therefore enables the simpler analysis used in the main text.

```
persp<-
aggregate(loglambda~animal+invasive.category,mean,data=invas)
persp$loginertiaup<-
aggregate(loginertiaup~animal+invasive.category,mean,data=invas)
$loginertiaup
persp$loginertiadown<-
aggregate(loginertiadown~animal+invasive.category,mean,data=inva
s)$loginertiadown
persp$logmaxatt<-
aggregate(logmaxatt~animal+invasive.category,mean,data=invas)$lo
gmaxatt
persp$logreac<-
aggregate(logreac~animal+invasive.category,mean,data=invas)$logr
eac
persp$n<-aggregate(n~animal+invasive.category,mean,data=invas)$n
persp$Species<-persp$animal
```

Save the invas and persp dataframes prior to modeling

```
write.csv(invas, paste0(direc,"mcmc_data_invasives.csv"))
write.csv(persp,paste0(direc,"per_species_data.csv"))
```

2.5 R code to fit models to the data

Some information on the Bayesian models used:

- Response variables have been logged to ensure that they are Gaussian
- The animal random effect is the phylogeny
- For models of the invas dataframe Species is additionally included as a random effect as we have multiple populations per species
- Burnin of 10% interations and a thinning interval of <0.1% iterations for Markov chains (ideally you need an effective sample size of at least 1000: to be safe can make thinning <0.05%)
- Proper uninformative priors are used (nu is small but >0). In this example we use parameter expansion (alpha.mu and alpha.V) as some of the chains got stuck at 0. We don’t need to

specify fixed effect priors as MCMCglmm does a good job of picking default one but if we did they'd be specified as B. G is the random effects - the number of G structures should match the number of random effects. If you use random effects interaction or regression, V should be changed to an identity matrix of the same dimension as the number of parameters to estimate. R is the residuals. Parameter expansion for residual priors is not supported (but I've never seen it needed). It doesn't matter what order you put B, G and R in but G1, G2, G3,… must be in the same order as specified for random effects in the model

- (verbose=F can stop the models updating in real time)

2.5.1 Fit Bayesian hierarchical models to the persp dataset (same analysis as the main paper; models the mean for each species)

Model A1 - persp model for log lambda

- Set priors

```
prior1.loglambda<-list(R = list(V = 1, nu=0.001),
                G = list(G1=list(V = 1, nu=0.001, alpha.mu=0,
alpha.V=100)))
```

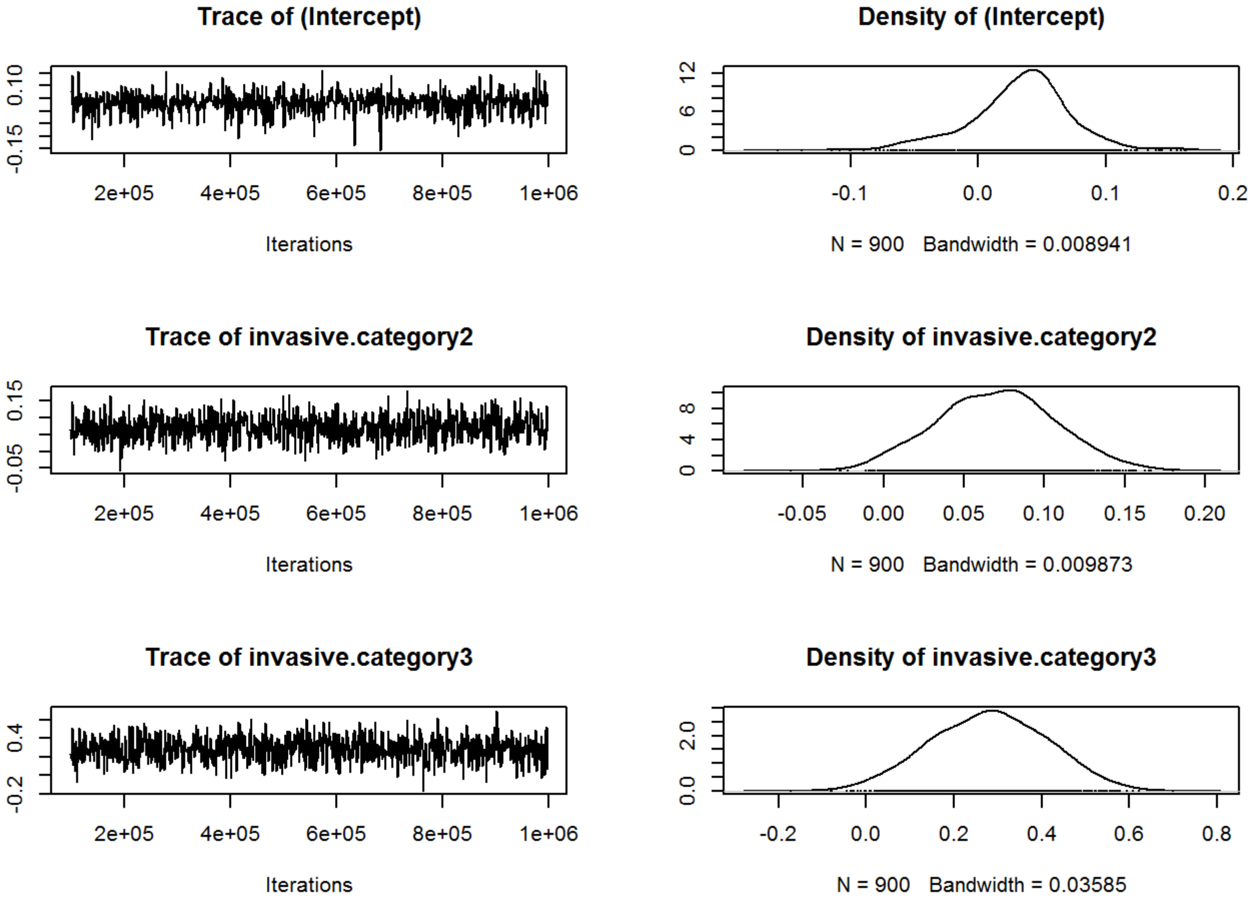
- Run model

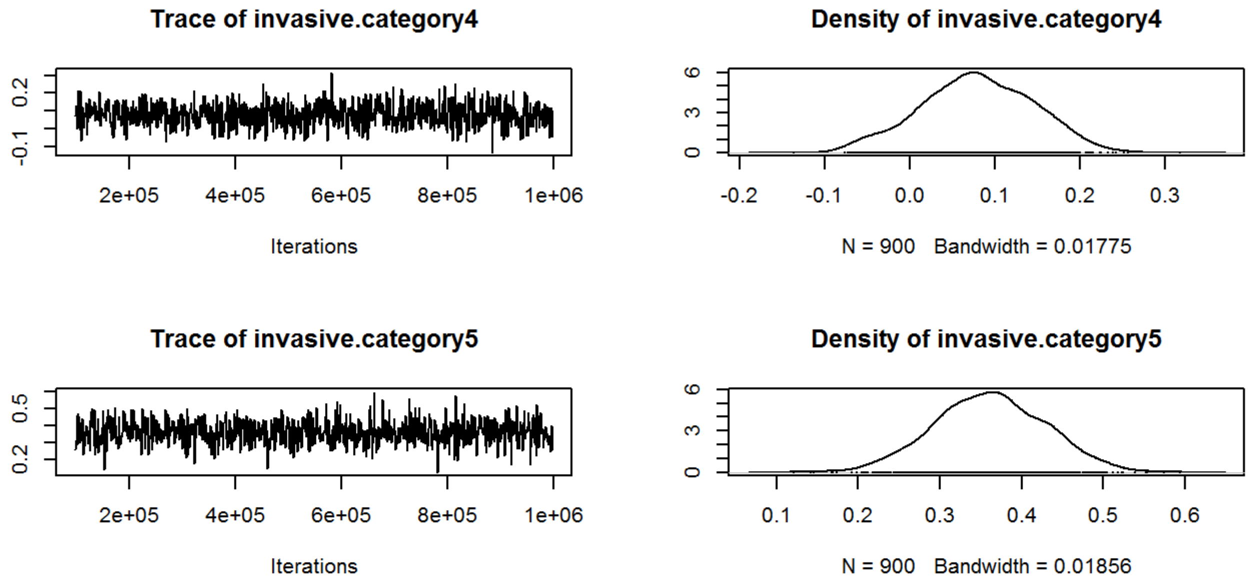
```
m1.loglambda<-MCMCglmm(loglambda ~ invasive.category,
                       random=~animal, family="gaussian",
                       prior=prior1.loglambda, data=persp,
pedigree=compadre.tree, nodes="TIPS",
                       thin=1000, nitt=1000000, burnin=100000,
verbose=T)
```

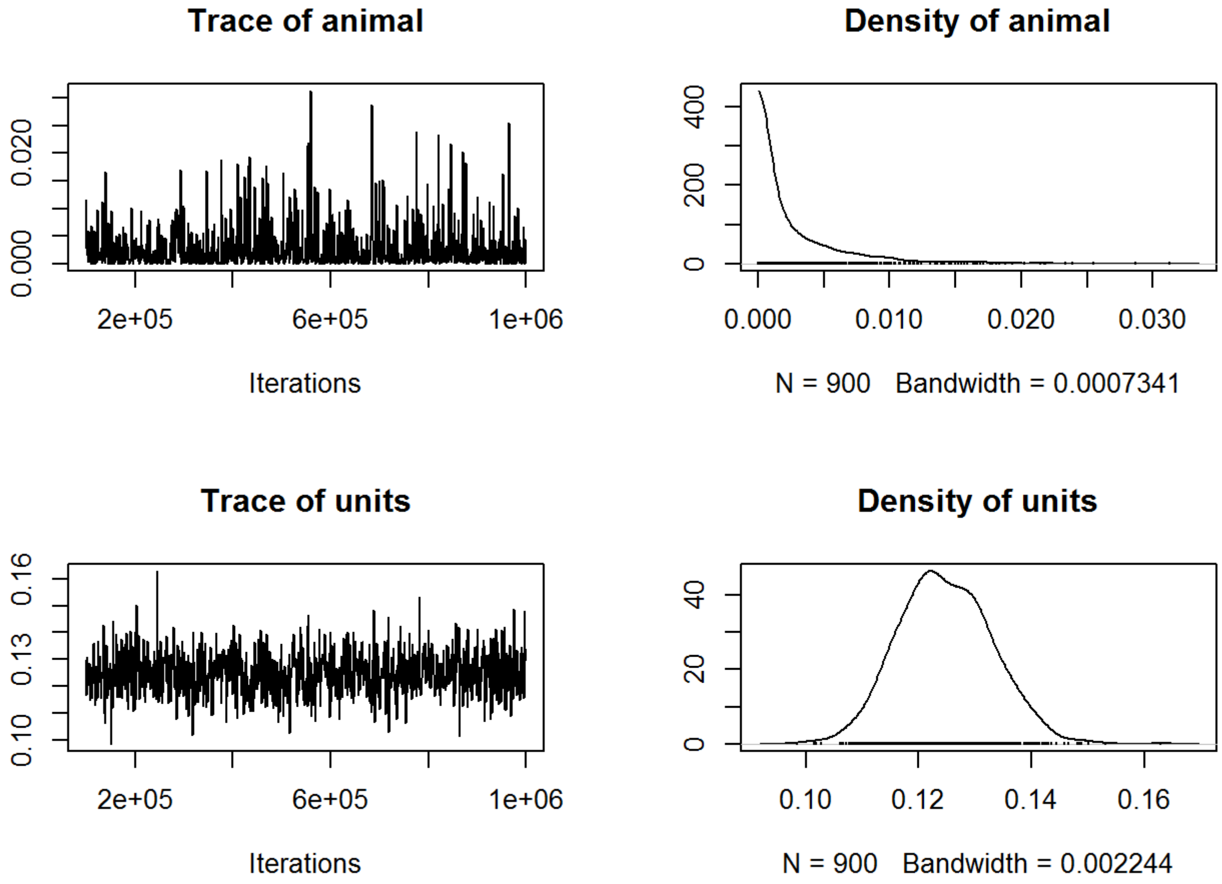
- Model summary and plots

```
summary(m1.loglambda)
##
##  Iterations = 100001:999001
##  Thinning interval  = 1000
##  Sample size  = 900
##
##  DIC: 385.1425
##
##  G-structure:  ~animal
##
##        post.mean  l-95% CI u-95% CI eff.samp
## animal  0.002955 4.433e-10   0.0112      900
##
```

```
##  R-structure:  ~units
##
##        post.mean l-95% CI u-95% CI eff.samp
## units    0.1247     0.11   0.1414      900
##
##  Location effects: loglambda ~ invasive.category
##
##                     post.mean  l-95% CI  u-95% CI eff.samp
pMCMC
## (Intercept)          0.032434 -0.051554  0.111977      900
0.3444
## invasive.category2  0.069811 -0.001252  0.137855      900
0.0489 *
## invasive.category3  0.280139  0.022420  0.522746      900
0.0333 *
## invasive.category4  0.079420 -0.050370  0.200732     1029
0.2178
## invasive.category5  0.360827  0.236578  0.501369     1234
<0.001 **
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' '
1
plot(m1.loglambda)
```




Trace of invasive.category4
-0.1
0.2
2e+05
4e+05
6e+05
8e+05
1e+06
Iterations
Density of invasive.category4
0
3
6
-0.2
-0.1
0.0
0.1
0.2
0.3
N = 900   Bandwidth = 0.01775
Trace of invasive.category5
0.2
0.5
2e+05
4e+05
6e+05
8e+05
1e+06
Iterations
Density of invasive.category5
0
3
6
0.1
0.2
0.3
0.4
0.5
0.6
N = 900   Bandwidth = 0.01856


Trace of animal
0.000
0.020
2e+05
6e+05
1e+06
Iterations
Density of animal
0
200
400
0.000
0.010
0.020
0.030
N = 900   Bandwidth = 0.0007341
Trace of units
0.10
0.13
0.16
2e+05
6e+05
1e+06
Iterations
Density of units
0
20
40
0.10
0.12
0.14
0.16
N = 900   Bandwidth = 0.002244

Model A2 - persp model for log inertiaup.

- Set priors

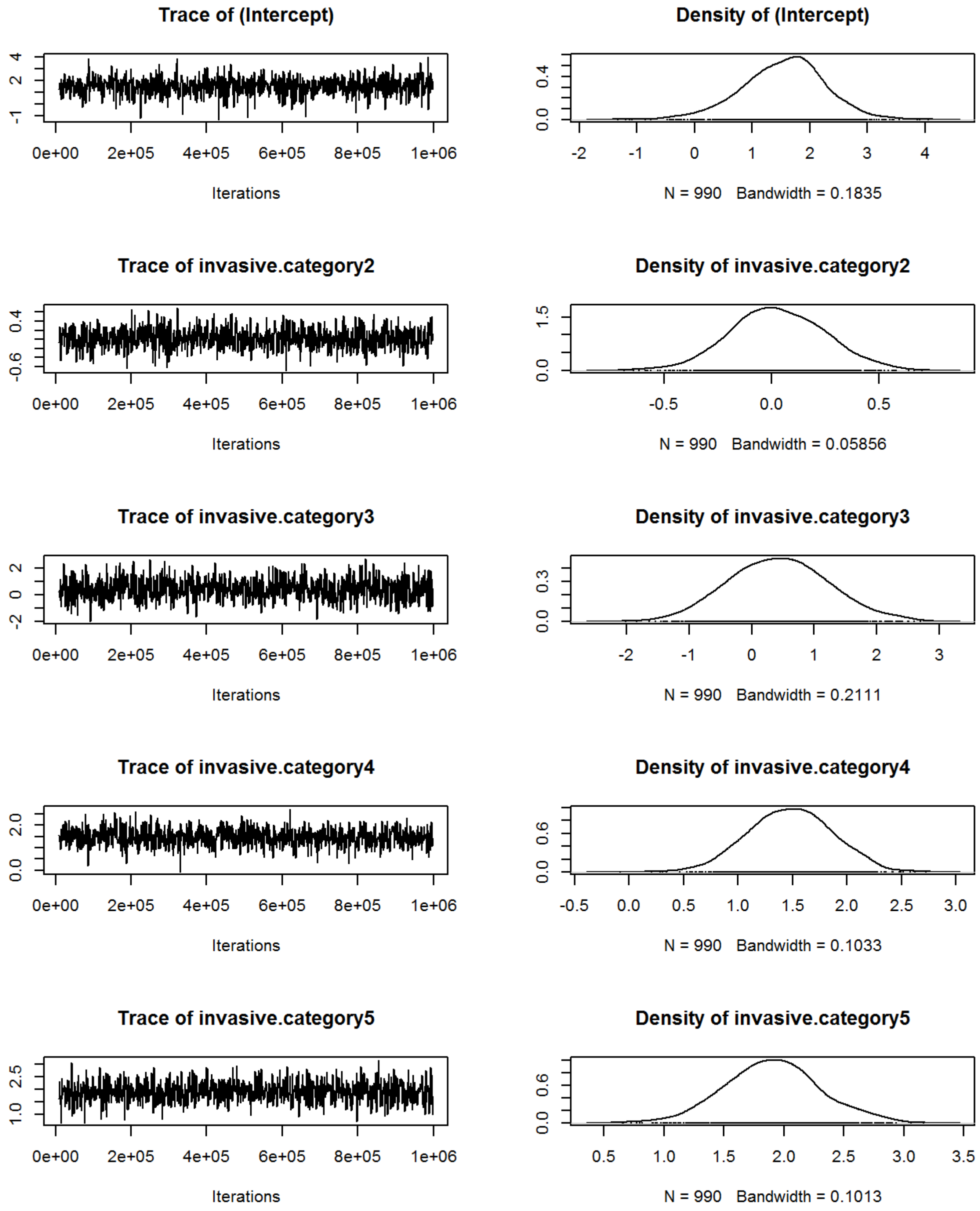
```
prior1.inertiaup<-list(R = list(V = 1, nu=0.001),
                       G = list(G1=list(V = 1, nu=0.001, alpha.mu=0,
alpha.V=100)))
```

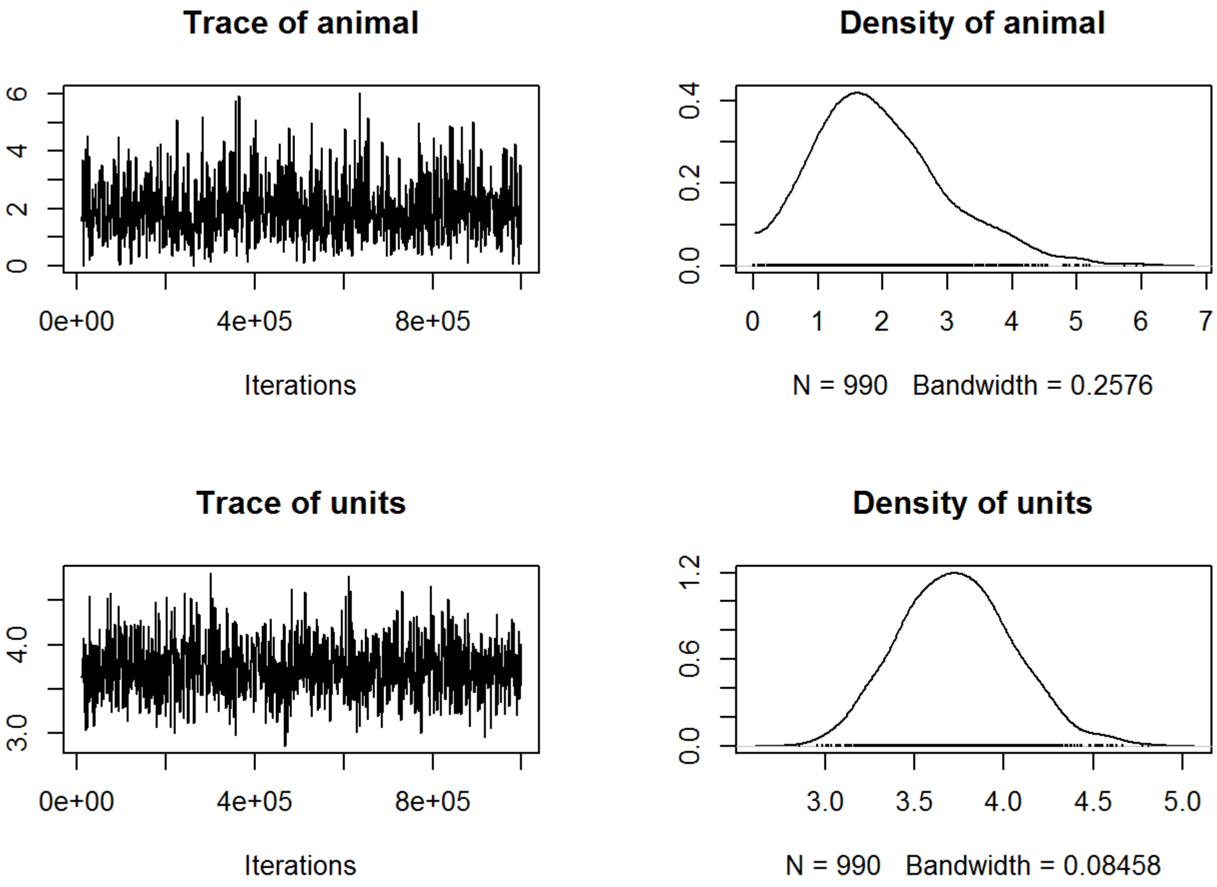
- Run model

```
m1.loginertiaup<-MCMCglmm(loginertiaup ~ invasive.category,
                          random=~animal, family="gaussian",
                          prior=prior1.inertiaup, data=persp,
pedigree=compadre.tree, nodes="TIPS",
                          thin=1000, nitt=1000000, burnin=10000,
verbose=T)
```

- Model summary and plots.

```
summary(m1.loginertiaup)
##
##  Iterations = 10001:999001
##  Thinning interval  = 1000
##  Sample size  = 990
##
##  DIC: 2105.212
##
##  G-structure:  ~animal
##
##        post.mean l-95% CI u-95% CI eff.samp
## animal     1.974   0.3325    4.143      990
##
##  R-structure:  ~units
##
##       post.mean l-95% CI u-95% CI eff.samp
## units     3.735    3.167    4.376      990
##
##  Location effects: loginertiaup ~ invasive.category
##
##                      post.mean  l-95% CI  u-95% CI eff.samp
pMCMC
## (Intercept)           1.538215  0.003007  2.898646      990
0.04848 *
## invasive.category2  0.027819 -0.358728  0.485069      990
0.91717
## invasive.category3  0.432632 -1.129706  1.946748      990
0.61212
## invasive.category4  1.476345  0.794881  2.222330      990
0.00202 **
## invasive.category5  1.903945  1.190630  2.732268     1187 <
0.001 **
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' '
1
plot(m1.loginertiaup)
```


Trace of (Intercept)
-1
2
4
0e+00
2e+05
4e+05
6e+05
8e+05
1e+06
Iterations
Density of (Intercept)
0.0
0.4
-2
-1
0
1
2
3
4
N = 990 Bandwidth = 0.1835
Trace of invasive.category2
-0.6
0.4
0e+00
2e+05
4e+05
6e+05
8e+05
1e+06
Iterations
Density of invasive.category2
0.0
1.5
-0.5
0.0
0.5
N = 990 Bandwidth = 0.05856
Trace of invasive.category3
-2
0
2
0e+00
2e+05
4e+05
6e+05
8e+05
1e+06
Iterations
Density of invasive.category3
0.0
0.3
-2
-1
0
1
2
3
N = 990 Bandwidth = 0.2111
Trace of invasive.category4
0.0
2.0
0e+00
2e+05
4e+05
6e+05
8e+05
1e+06
Iterations
Density of invasive.category4
0.0
0.6
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
3.0
N = 990 Bandwidth = 0.1033
Trace of invasive.category5
1.0
2.5
0e+00
2e+05
4e+05
6e+05
8e+05
1e+06
Iterations
Density of invasive.category5
0.0
0.6
0.5
1.0
1.5
2.0
2.5
3.0
3.5
N = 990 Bandwidth = 0.1013



Model A3 - persp model for log inertiadown.

- Set priors

```
prior1.inertiadown<-list(R = list(V = 1, nu=0.001),
                  G = list(G1=list(V = 1, nu=0.001, alpha.mu=0,
alpha.V=100)))
```

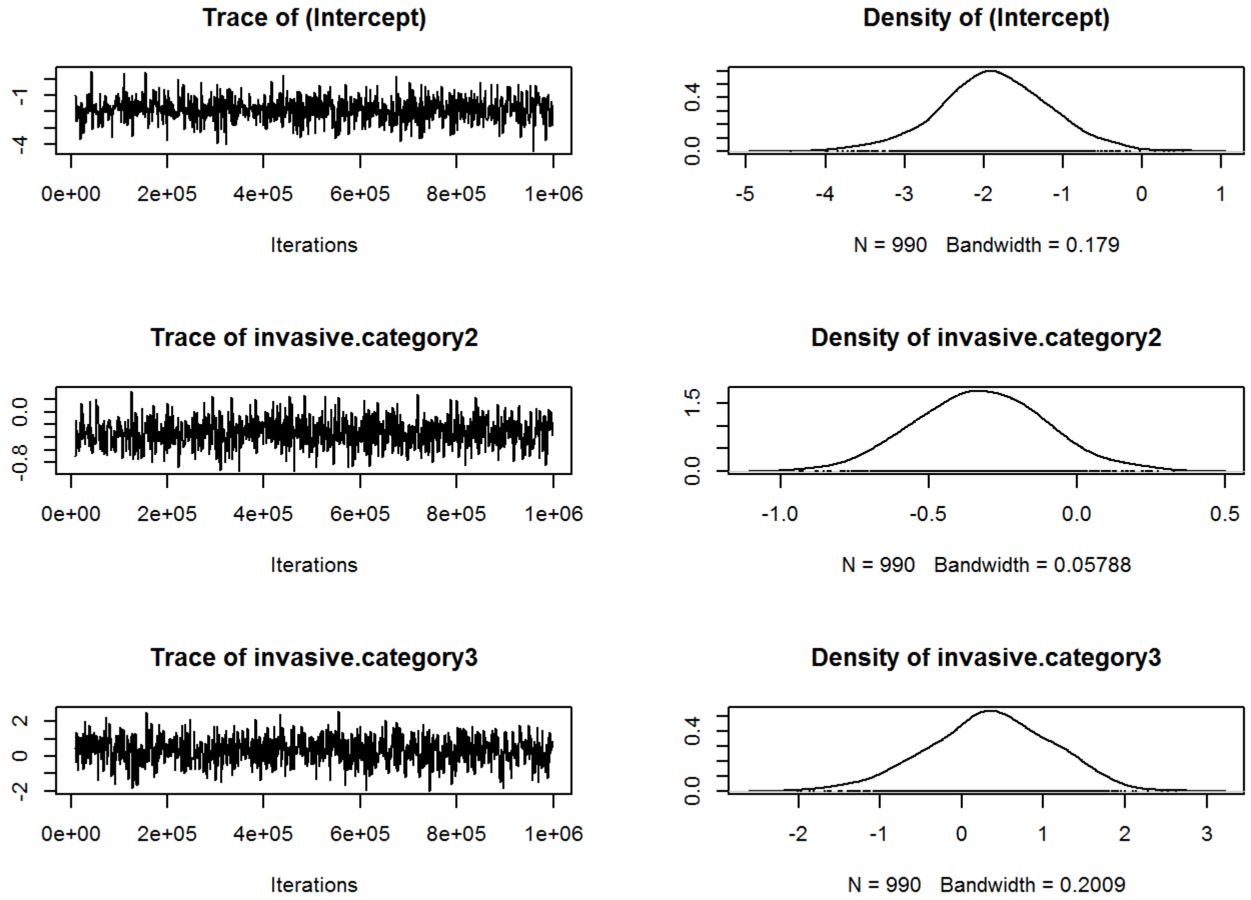
- Run model

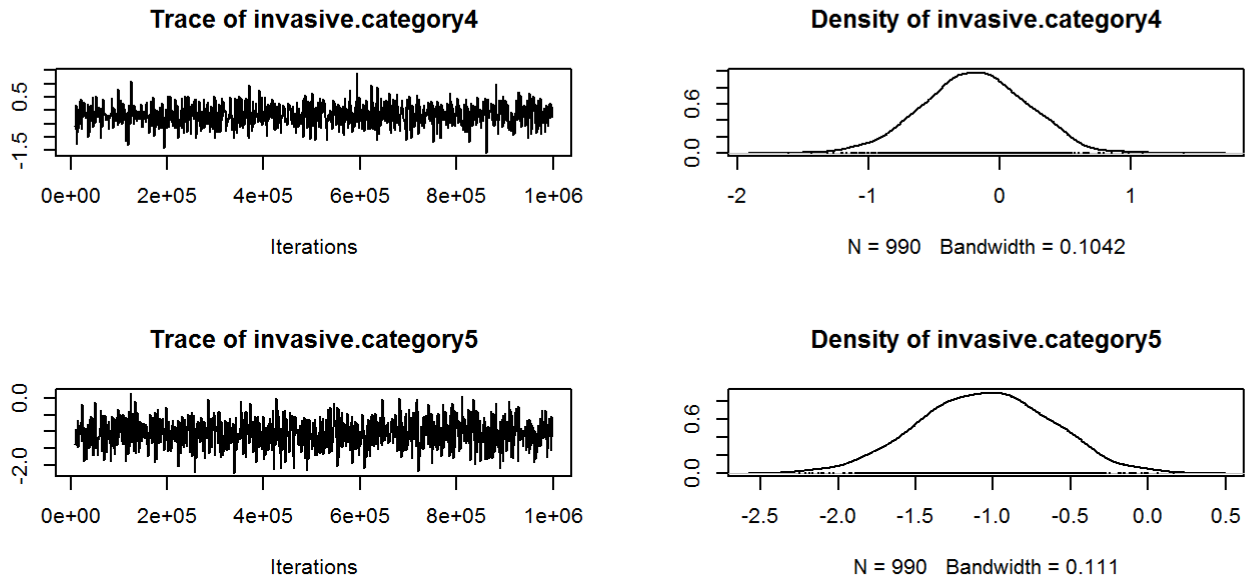
```
m1.loginertiadown<-MCMCglmm(loginertiadown ~ invasive.category,
                           random=~animal, family="gaussian",
                           prior=prior1.inertiadown, data=persp,
pedigree=compadre.tree, nodes="TIPS",
                           thin=1000, nitt=1000000, burnin=10000,
verbose=T)
```

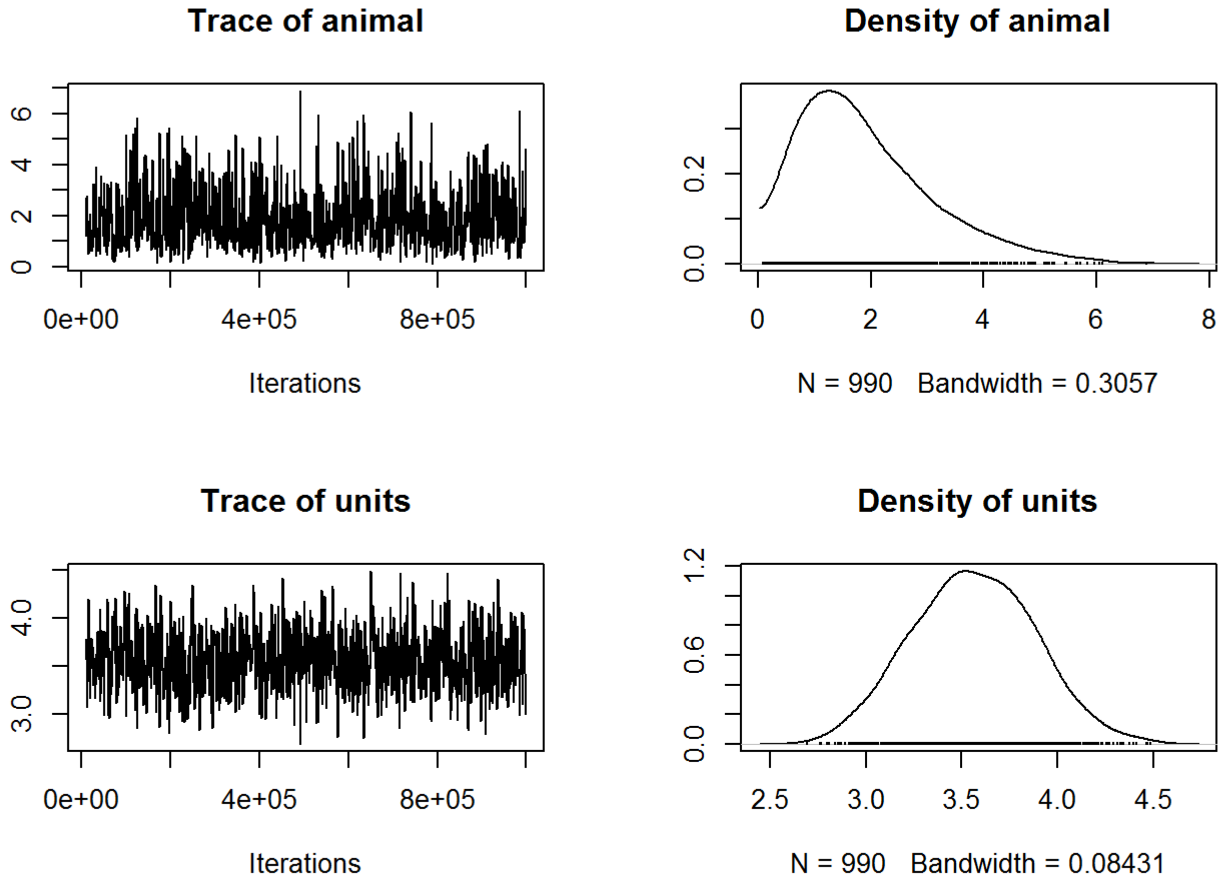
- Model summary and plots

```
summary(m1.loginertiadown)
##
##  Iterations = 10001:999001
##  Thinning interval  = 1000
##  Sample size  = 990
##
##  DIC: 2083.936
```

```
##
##  G-structure:  ~animal
##
##         post.mean l-95% CI u-95% CI eff.samp
## animal      1.907   0.1233    4.251    885.7
##
##  R-structure:  ~units
##
##       post.mean l-95% CI u-95% CI eff.samp
## units     3.561    2.923    4.137      990
##
##  Location effects: loginertiadown ~ invasive.category
##
##                      post.mean l-95% CI u-95% CI eff.samp
pMCMC
## (Intercept)           -1.8635  -3.1339  -0.3214       990
0.01010 *
## invasive.category2   -0.3253  -0.7500   0.1039       990
0.13131
## invasive.category3    0.3450  -1.0748   1.8055       990
0.61010
## invasive.category4   -0.1854  -0.8939   0.5547      1619
0.63232
## invasive.category5   -1.0534  -1.8892  -0.3296       990
0.00404 **
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' '
1
plot(m1.loginertiadown)
```




Trace of invasive.category4
-1.5
0.5
0e+00
2e+05
4e+05
6e+05
8e+05
1e+06
Iterations
Density of invasive.category4
0.0
0.6
-2
-1
0
1
N = 990 Bandwidth = 0.1042
Trace of invasive.category5
-2.0
0.0
0e+00
2e+05
4e+05
6e+05
8e+05
1e+06
Iterations
Density of invasive.category5
0.0
0.6
-2.5
-2.0
-1.5
-1.0
-0.5
0.0
0.5
N = 990 Bandwidth = 0.111


Trace of animal
0
2
4
6
0e+00
4e+05
8e+05
Iterations
Density of animal
0.0
0.2
0
2
4
6
8
N = 990 Bandwidth = 0.3057
Trace of units
3.0
4.0
0e+00
4e+05
8e+05
Iterations
Density of units
0.0
0.6
1.2
2.5
3.0
3.5
4.0
4.5
N = 990 Bandwidth = 0.08431

2.5.2 Fit Bayesian hierarchical models to the invas dataset (full analysis including multiple populations of each species)

Model B1 - invas model for log lambda

- Set priors

```
prior2.2<-list(R = list(V = 1, nu=0.001),
               G = list(G1=list(V = 1, nu=0.001, alpha.mu=0,
alpha.V=100),
                        G2=list(V = 1, nu=0.001, alpha.mu=0,
alpha.V=100)))
```

- Run model

```
m2.loglambda<-MCMCglmm(loglambda ~ invasive.category,
                       random=~Species + animal,
family="gaussian",
                       prior=prior2.2, data=invas,
pedigree=compadre.tree, nodes="TIPS",
                       thin=1000, nitt=1000000, burnin=10000,
verbose=T)
```

- Model summary and plots

```
summary(m2.loglambda)
##
##  Iterations = 10001:999001
##  Thinning interval  = 1000
##  Sample size  = 990
##
##  DIC: 654.8935
##
##  G-structure:  ~Species
##
##         post.mean l-95% CI u-95% CI eff.samp
## Species   0.05434  0.04101  0.06879      990
##
##                ~animal
##
##        post.mean  l-95% CI u-95% CI eff.samp
## animal  0.002133 6.653e-09 0.008551      990
##
##  R-structure:  ~units
##
##       post.mean l-95% CI u-95% CI eff.samp
## units   0.08311  0.07442  0.09223     1280
##
##  Location effects: loglambda ~ invasive.category
##
##                         post.mean  l-95% CI  u-95% CI eff.samp
```

```
pMCMC
## (Intercept)         0.039162 -0.042109  0.100949      990
0.2242
## invasive.category2  0.052481 -0.006726  0.112233      990
0.0848 .
## invasive.category3  0.288665  0.069605  0.559751     1272
0.0263 *
## invasive.category4 -0.015866 -0.123316  0.106505      990
0.7838
## invasive.category5  0.345833  0.230776  0.466968      990
<0.001 **
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' '
1
#plot(m1.loglambda)
```

Model B2 - invas model for log inertiaup

- Set priors

```
prior2.inertiaup<-list(R = list(V = 1, nu=0.001),
               G = list(G1=list(V = 1, nu=0.001, alpha.mu=0,
alpha.V=100),
                        G2=list(V = 1, nu=0.001, alpha.mu=0,
alpha.V=100)))
```

- Run model

```
m2.inertiaup_full<-MCMCglmm(loginertiaup ~ invasive.category,
                            random=~Species + animal,
family="gaussian",
                            prior=prior2.inertiaup, data=invas,
pedigree=compadre.tree, nodes="TIPS",
                            thin=10, nitt=10000, burnin=1000,
verbose=T)
```

- Model summary and plots

```
summary(m2.inertiaup_full)
##
##  Iterations = 1001:9991
##  Thinning interval  = 10
##  Sample size  = 900
##
##  DIC: 3080.577
##
##  G-structure:  ~Species
##
##         post.mean l-95% CI u-95% CI eff.samp
## Species     3.385     2.77    4.052    230.3
##
##                ~animal
##
##        post.mean l-95% CI u-95% CI eff.samp
## animal     1.921   0.1467    3.913    101.1
```

```
##
##  R-structure:  ~units
##
##       post.mean l-95% CI u-95% CI eff.samp
## units    0.5875   0.5315   0.6568      900
##
##  Location effects: loginertiaup ~ invasive.category
##
##                      post.mean l-95% CI u-95% CI eff.samp
pMCMC
## (Intercept)           1.49122  0.01225  2.85042    758.4
0.04667 *
## invasive.category2   0.01621 -0.21665  0.27824   1585.0
0.86667
## invasive.category3   0.48261 -1.04640  2.06986    900.0
0.53778
## invasive.category4   0.84698  0.24793  1.47723    900.0
0.00667 **
## invasive.category5   2.43134  1.79585  3.19005   1153.2 <
0.001 **
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' '
1
#plot(m2.inertiaup_full)
```

Model B3 - persp model for log inertia down

- Set priors

```
prior2.inertiadown<-list(R = list(V = 1, nu=0.001),
               G = list(G1=list(V = 1, nu=0.001, alpha.mu=0,
alpha.V=100),
                        G2=list(V = 1, nu=0.001, alpha.mu=0,
alpha.V=100)))
```

- Run model

```
m2.inertiadown_full<-MCMCglmm(loginertiadown ~
invasive.category,
                            random=~Species + animal,
family="gaussian",
                            prior=prior2.inertiadown,
data=invas, pedigree=compadre.tree, nodes="TIPS",
                            thin=10, nitt=10000, burnin=1000,
verbose=T)
```

- Model summary and plots

```
summary(m2.inertiadown_full)
##
##  Iterations = 1001:9991
##  Thinning interval  = 10
##  Sample size  = 900
##
##  DIC: 4419.331
```

```
##
##  G-structure:  ~Species
##
##         post.mean l-95% CI u-95% CI eff.samp
## Species     2.165    1.584    2.705    484.2
##
##                ~animal
##
##        post.mean l-95% CI u-95% CI eff.samp
## animal     1.664   0.2008    3.352    243.2
##
##  R-structure:  ~units
##
##       post.mean l-95% CI u-95% CI eff.samp
## units     2.087    1.886     2.31      900
##
##  Location effects: loginertiadown ~ invasive.category
##
##                    post.mean l-95% CI u-95% CI eff.samp
pMCMC
## (Intercept)          -1.78177 -3.12718 -0.44235      900
0.00889 **
## invasive.category2  -0.34916 -0.71993 -0.01106      900
0.05333 .
## invasive.category3   0.25828 -1.25052  1.78909      900
0.74444
## invasive.category4  -0.26967 -0.93824  0.42057      900
0.42667
## invasive.category5  -0.96815 -1.70601 -0.22511      900
0.01333 *
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' '
1
#plot(m2.inertiadown_full)
```

2.5.3 Equivalent non-bayesian models to demonstrate robustness of the results

The first set of models are lme models of the full dataset (invas) with Species as a random effect and no phylogenetic random effect 1.Log lambda 2.Log inertia_up 3.Log inertia_down.

```
lmm1<-lme(loglambda~invasive.category-
1,random=~1|Species,data=invas)
summary(lmm1)
## Linear mixed-effects model fit by REML
##  Data: invas
##        AIC      BIC    logLik
##   820.4189 855.7149 -403.2095
##
## Random effects:
##  Formula: ~1 | Species
##         (Intercept)  Residual
## StdDev:   0.2334153 0.2879874
##
## Fixed effects: loglambda ~ invasive.category - 1
```

```
##                         Value  Std.Error  DF  t-value p-value
## invasive.category1 0.0444132 0.01846766 669 2.404920  0.0164
## invasive.category2 0.0990506 0.02593653 669 3.818962  0.0001
## invasive.category3 0.3350964 0.12635809 476 2.651958  0.0083
## invasive.category4 0.0348412 0.05820372 669 0.598608  0.5496
## invasive.category5 0.3973969 0.05992668 669 6.631385  0.0000
##  Correlation:
##                    invs.1 invs.2 invs.3 invs.4
## invasive.category2 0.116
## invasive.category3 0.000  0.000
## invasive.category4 0.008  0.009  0.000
## invasive.category5 0.002  0.001  0.000  0.061
##
## Standardized Within-Group Residuals:
##          Min           Q1          Med           Q3
Max
## -11.07995370  -0.21684285  -0.05292606   0.14356594
5.78562628
##
## Number of Observations: 1149
## Number of Groups: 477
lmm2<-lme(loginertiaup~invasive.category-
1,random=~1|Species,data=invas)
summary(lmm2)
## Linear mixed-effects model fit by REML
##  Data: invas
##        AIC      BIC    logLik
##   3875.488 3910.784 -1930.744
##
## Random effects:
##  Formula: ~1 | Species
##         (Intercept)  Residual
## StdDev:    1.988774 0.7641179
##
## Fixed effects: loginertiaup ~ invasive.category - 1
##                        Value Std.Error  DF   t-value p-value
## invasive.category1 1.914866 0.1083867 669 17.666989  0.0000
## invasive.category2 1.888029 0.1361188 669 13.870449  0.0000
## invasive.category3 1.950332 0.7935277 476  2.457799  0.0143
## invasive.category4 2.633894 0.3010887 669  8.747900  0.0000
## invasive.category5 4.249800 0.3392491 669 12.527078  0.0000
##  Correlation:
##                    invs.1 invs.2 invs.3 invs.4
## invasive.category2 0.466
## invasive.category3 0.000  0.000
## invasive.category4 0.060  0.063  0.000
## invasive.category5 0.027  0.023  0.000  0.291
##
## Standardized Within-Group Residuals:
##         Min          Q1         Med          Q3         Max
## -5.48168503 -0.28091537 -0.05988362  0.27441028  7.65981168
##
## Number of Observations: 1149
## Number of Groups: 477
lmm3<-lme(loginertiadown~invasive.category-
1,random=~1|Species,data=invas)
summary(lmm3)
## Linear mixed-effects model fit by REML
```

```
##  Data: invas
##        AIC      BIC    logLik
##   4696.936 4732.232 -2341.468
##
## Random effects:
##  Formula: ~1 | Species
##         (Intercept) Residual
## StdDev:     1.64083 1.441664
##
## Fixed effects: loginertiadown ~ invasive.category - 1
##                        Value Std.Error  DF    t-value p-value
## invasive.category1 -1.983616 0.1118658 669 -17.732100  0.0000
## invasive.category2 -2.216874 0.1562470 669 -14.188265  0.0000
## invasive.category3 -1.604859 0.7749331 476  -2.070965  0.0389
## invasive.category4 -2.151217 0.3459838 669  -6.217682  0.0000
## invasive.category5 -2.792004 0.3661520 669  -7.625261  0.0000
##  Correlation:
##                    invs.1 invs.2 invs.3 invs.4
## invasive.category2 0.178
## invasive.category3 0.000  0.000
## invasive.category4 0.014  0.016  0.000
## invasive.category5 0.004  0.002  0.000  0.098
##
## Standardized Within-Group Residuals:
##         Min          Q1         Med          Q3         Max
## -10.3863042  -0.1932449   0.1050737   0.3416646   5.6618074
##
## Number of Observations: 1149
## Number of Groups: 477
```

The second set of models are ordinary linear models run in the persp dataset

```
lm1<-glm(loglambda~invasive.category,data=persp)
summary(lm1)
##
## Call:
## glm(formula = loglambda ~ invasive.category, data = persp)
##
## Deviance Residuals:
##      Min        1Q    Median        3Q       Max
## -1.62993  -0.10537  -0.04395   0.03524   2.67676
##
## Coefficients:
##                     Estimate Std. Error t value Pr(>|t|)
## (Intercept)          0.04428    0.02033   2.178   0.0299 *
## invasive.category2  0.07018    0.03752   1.870   0.0620 .
## invasive.category3  0.27825    0.13532   2.056   0.0403 *
## invasive.category4  0.07681    0.06675   1.151   0.2504
## invasive.category5  0.36097    0.06992   5.163 3.54e-07 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' '
1
##
## (Dispersion parameter for gaussian family taken to be
0.125292)
##
##     Null deviance: 65.292  on 494  degrees of freedom
```

```
## Residual deviance: 61.393  on 490  degrees of freedom
## AIC: 383.56
##
## Number of Fisher Scoring iterations: 2
lm2<-glm(loginertiaup~invasive.category,data=persp)
summary(lm2)
##
## Call:
## glm(formula = loginertiaup ~ invasive.category, data = persp)
##
## Deviance Residuals:
##     Min       1Q   Median       3Q      Max
## -3.5243  -1.4262  -0.6103   0.8082  10.5285
##
## Coefficients:
##                     Estimate Std. Error t value Pr(>|t|)
## (Intercept)          1.91587    0.11896  16.105  < 2e-16 ***
## invasive.category2 -0.11528    0.21951  -0.525 0.599714
## invasive.category3  0.01402    0.79167   0.018 0.985875
## invasive.category4  1.35494    0.39049   3.470 0.000567 ***
## invasive.category5  1.71052    0.40902   4.182 3.42e-05 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' '
1
##
## (Dispersion parameter for gaussian family taken to be
4.288145)
##
##     Null deviance: 2230.2  on 494  degrees of freedom
## Residual deviance: 2101.2  on 490  degrees of freedom
## AIC: 2132.4
##
## Number of Fisher Scoring iterations: 2
lm3<-glm(loginertiadown~invasive.category-1,data=persp)
summary(lm3)
##
## Call:
## glm(formula = loginertiadown ~ invasive.category - 1, data =
persp)
##
## Deviance Residuals:
##      Min        1Q    Median        3Q       Max
## -14.9352   -0.5543    0.5028    1.2433    2.4229
##
## Coefficients:
##                     Estimate Std. Error t value Pr(>|t|)
## invasive.category1  -1.9986     0.1163 -17.177  < 2e-16 ***
## invasive.category2  -2.1686     0.1804 -12.020  < 2e-16 ***
## invasive.category3  -1.5503     0.7655  -2.025   0.0434 *
## invasive.category4  -2.0722     0.3637  -5.697 2.11e-08 ***
## invasive.category5  -2.8805     0.3827  -7.526 2.53e-13 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' '
1
##
## (Dispersion parameter for gaussian family taken to be
4.101718)
##
```

```
##     Null deviance: 4194.9  on 495  degrees of freedom
## Residual deviance: 2009.8  on 490  degrees of freedom
## AIC: 2110.4
##
## Number of Fisher Scoring iterations: 2
```

4. Supplementary Material: Results

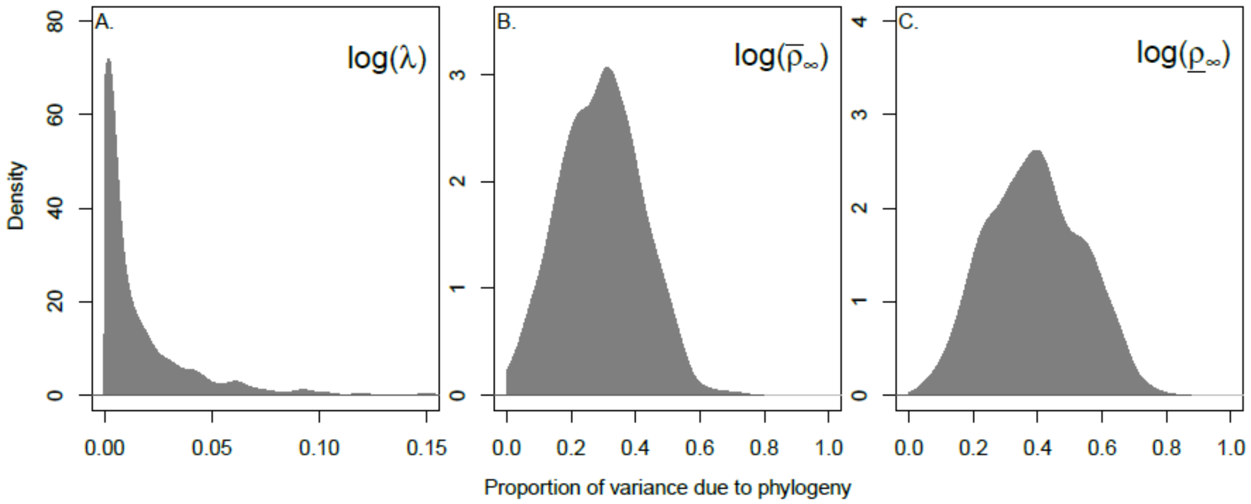


Fig. S1. Phylogenetic signal in three demographic metrics. (A) stable rate of population increase (log (λ)); (B) upper bound on demographic inertia (log($\bar{\rho}_\infty$)) and (C) lower bound on demographic inertia (log($\underline{\rho}_\infty$)). Posterior, probability density distributions of the proportion of residual variance absorbed by the phylogenetic covariance matrix in the MCMCglmm models represented in Figure 2 of the main text. These figures demonstrate that phylogenetic signal in stable population growth rate is not credibly different from zero (A). However, we see credible non-zero phylogenetic signal in demographic amplification (B), and in demographic attenuation (C).

Generalised Least Square:

Below we present the downscaled generalised least squares regression models with phylogenetic correlation structure (PGLS). We find no signal of phylogenetic patterns between log(λ) and invasiveness (χ^2 1df = 0.097, p=0.756). We do find signal of phylogenetic patterns between log($\bar{\rho}_\infty$) and invasiveness (χ^2 1df = 8.788, p=0.003), and also between log($\underline{\rho}_\infty$) and invasiveness (χ^2 1df = 5.294, p=0.021). This analysis replicated the patterns observed in the MCMCglmm analyses, and confirmed the significant influence of invasion category on log(λ) (χ^2 4df = 49.657, p<0.001), on log($\bar{\rho}_\infty$) (χ^2 4df = 41.809, p<0.001), and on log($\underline{\rho}_\infty$) (χ^2 4df = 14.816, p=0.005). Inclusion of the number of lifestages within the model confirms that number of lifestages has no influence on log(λ) (χ^2 1df = 0.324, p=569); but influences both log($\bar{\rho}_\infty$) (χ^2 1df = 42.325, p<0.001) and log($\underline{\rho}_\infty$) (χ^2 1df = 23.134, p<0.001).

Linear Mixed-Effect Models:

Below we present linear mixed-effects (LME) models of demographic metrics per population per species. These analyses ignore the phylogenetic patterning of the data, but confirmed the results of the MCMCglmm. These models again replicate the differences among categories and the patterns observed in the MCMCglmm, confirming a significant influence of invasion category on log (λ) (χ^2 4df = 41.876, p<0.001) and on log($\bar{\rho}_\infty$) (χ^2 4df = 49.021, p<0.001) but not on log($\underline{\rho}_\infty$) (χ^2 4df = 8.778, p=0.067).

General Linear Models:

Below we present general linear models (GLM) of demographic metrics per species. These analyses ignore the phylogenetic patterning of the data, but again confirmed the results of the MCMCglmm. These models confirm the significant effect of the invasion category on log(λ) (F 4,493 = 17.792, p<0.001) and on log($\bar{\rho}_\infty$) (F4,493 = 7.6982, p<0.001) but not on log($\underline{\rho}_\infty$) (F 4,493 = 1.711, p=0.146).

Pseudo R^2 Values:

Here we present the Pseudo R^2 values that measure the proportion of non-phylogenetic variance that is absorbed by the fixed effect (=$\text{vari}_{\text{fixed}}$ / ($\text{var}_{\text{fixed}}$+$\text{var}_{\text{resid}}$)); these are presented in Table SM4 below.

Table SM4: Table of Variance Components and Pseudo R^2 Values.

	Fixed Effects	Species	Residuals	Pseudo R^2 Value
(λ)	0.034	0.062	0.083	0.291
($\bar{\rho}_\infty$)	1.127	3.781	0.570	0.664
($\underline{\rho}_\infty$)	1.135	2.573	2.039	0.358

The pseudo R^2 value for the three GLMs is 29% for log(λ), 66% for log($\bar{\rho}_\infty$) and 36% for log($\underline{\rho}_\infty$). Our observation that invasion category explains two thirds of the variation in demographic amplification provides further evidence of the important links between demographic responses to disturbance, and invasiveness.

Chapter 5:

Jelbert, K., Kendall, S. D. & Hodgson, D. Adapting to the invaded range: subtle changes in life history cause demographic change in invasive plants. In prep. target journal: Journal of Ecology.

Adapting to the invaded range: subtle changes in life history cause demographic change in invasive plants

Abstract

1. Invasive plants harm biodiversity, industry and human health. Predicting invasion success remains at the forefront of invasive species research yet it is not known whether invasive species exhibit range specific, demographic or life history differences that facilitate invasion.
2. We combined data from the COMPADRE Plant Matrix Database with new field data, to compare ten metrics of invasive plant populations, using seven species measured in both the invaded and native range. Metrics comprised vital rates (stage-specific recruitment, stasis & progression), demographic properties (stable population growth rate, and indices of transient dynamics, population inertia and reactivity) and selection potentials (elasticity of population growth rate to changes in vital rates). We tested whether invasive plant populations show changes in these metrics in the invaded range.
3. Demographic properties changed between the native and invaded range, while vital rates and selection potentials did not. In the invaded range, invasive plants exhibited greater propensity to amplify in response to disturbance, than conspecific populations in the native range. Range comparisons of individual metrics revealed reactivity and the upper bound of inertia to be significantly higher amongst populations in the invaded range.
4. Invasive plant populations ‘amplify’ more readily in response to disturbance in the invaded range, indicating that plants allocate greater resources to growth and reproduction once freed from the constraints of the native range. Large amplification is a characteristic of plant life histories with high reproductive output. We suggest that demographic amplification, caused by subtle changes to vital rates across the entire life cycle, is an important promotor of invasiveness.

5. Synthesis: Demographic properties of populations can only change in response to changes in life history. We discuss how subtle changes in life history might translate to detectable changes in population dynamics, with a focus on transient responses to demographic disturbances. We advocate collection of demographic data for a greater number of species, of broad geographic origin, to permit further global range comparisons to inform policy and trade restrictions.

Keywords: demography, inertia, invaded range, invasive plant, native range, population projection matrix, reactivity, transient dynamics

Introduction

Invasive species are variously defined as species that are both naturalized outside of their native range, and which detrimentally impact biodiversity, industry and human health (Daehler, 2003, IUCN, 1999, Beck et al., 2008). The harmful impacts of invasive species and the economic costs of mitigating damages are well documented (Butchart et al., 2010, Paini et al., 2016, Pimentel et al., 2005, Williams et al., 2010). Research has focused on all aspects of invasion biology but two key questions continue to drive invasive species research: ‘do invasive species share a particular trait(s) that can be used to predict invasiveness?’ (Burns et al., 2013, Hovick et al., 2012, van Kleunen et al., 2010, Richardson and Pyšek, 2006) and ‘how can the deleterious impact of invasive species be curtailed?’ (Ramula et al., 2008, Hulme, 2009). An ability to predict which species will become invasive, and an understanding of the underlying mechanism of invasion is fundamental to successful containment and control.

Invasiveness is widespread amongst living organisms but here we focus on plants, which comprise one third of the top 100 of the world’s worst invasive species (Lowe et al., 2000). Among plants, invasive species research has revealed many putative correlates of invasiveness but has largely focused on individual demographic (Jelbert et al., 2015) and phenotypic traits (Schlaepfer et al., 2010), and environmental features which facilitate invasibility (Goodwin et al., 1999, Herron et al., 2007, Lambdon et al., 2008) yet both environmental variation (Buckley et al., 2010, Morris and Doak, 2005, Nantel et al., 1996) and species life history traits (Jelbert et al., 2015) act on invasiveness (proxies for which are abundance and spread rate) through their effect on stage-structured population dynamics (Harper and White, 1974).

To date, demographic studies have revealed life history traits specific to invasive species (Burns et al., 2013, Ramula et al., 2008). Invasive species exhibit greater rates of spread and projected population growth when compared with non-invasive species in the invaded range (Burns et al., 2013) and native species (Ramula et al., 2008). Invasive species exhibit greater fecundity per unit size when compared with non-invasive, native species in the native range (Jelbert et al., 2015) and conspecific native populations (Parker et al., 2013). Amongst simulated invading populations of both introduced and invasive species, highly fecund species exhibit more favourable transient dynamics (short-term population dynamics), greater long-term population growth and increased population viability (proxies of invasiveness) (Iles et al., 2016). Yet these demographic studies give no insight into how demographic processes may alter following introduction to a novel environment (invaded range) (c.f. Parker et al. (2013)).

It is well established that demographic parameters and predictions vary in response to the environment (Buckley et al., 2010, Morris and Doak, 2005, Nantel et al., 1996), and there is evidence that phenotypic and demographic traits such as seed size (Hierro et al., 2013, Graebner et al., 2012, Buckley et al., 2003) and fecundity (Parker et al., 2013) can increase in the invaded range. Yet few studies have compared the demography of invasive species between the invaded and native range (c.f. Hyatt and Araki (2006)). Hyatt and Araki (2006) compared the demography of *Polygonum perfoliatum* in the native and invaded range to reveal that population growth rate more frequently declined in the invaded range, and that amongst the growing invading and native populations, growth was driven by high rates of fecundity. Population growth was equally elastic to (affected by changes in) germination, fecundity, seed bank and survival in the invaded range but was most elastic to survival in the native range (Hyatt and Araki, 2006). These findings illustrate how the nature of disturbances experienced in each range cause populations to respond differently, and to be influenced by different vital rates.

In this study we use Population Projection Matrices (PPM) sourced from the COMPADRE Plant Matrix Database (COMPADRE 3.0.0) (Salguero-Gómez et al., 2014) or created from new field data, to compare the demography of seven invasive plant species between the native and invaded range to determine if demographic processes change between ranges. Population Projection Matrices divide life cycles into different life-stages, and contain life history information as vital rates (stage-specific recruitment, stasis & progression), selection potentials (elasticity of population growth rate to changes in vital rates) (StottFranco et al., 2010) and demographic properties (stable population growth rate, and the indices of transient dynamics, population inertia (ρ_∞) and reactivity) (Caswell, 2001). A classic comparative approach to identify predictors of invasion success is to compare vital rates or their elasticities (Hyatt and

Araki, 2006) but these are measured across the life cycle, and life cycles vary. Instead proxies such as stable stage distribution (SSD)-weighted means or elasticities are used but these assume a stable stage structure (SSS), whereby the population will grow or decline according to the stable growth rate (Caswell, 2001) and when disturbed away from the SSS will amplify or attenuate in the short-term, before returning to a stable rate of population increase or decline (Stott et al., 2011). Yet invasiveness is typically associated with disturbed environments (D'Antonio, Dudley & Mack 1999; Marvier, Kareiva & Neubert 2004), and therefore the assumption that invading populations will exhibit a SSS is inaccurate. We predict that those measures which assume a SSS will not be sufficiently sensitive to detect subtle demographic or life history differences that facilitate invasion. Indices of transient dynamics do not assume a SSS (Koons et al., 2007) and instead analyse what the population dynamics would be in a disturbed environment (Stott et al., 2011). We predict that analyses of transient indices will detect demographic or life history differences that enable invasion.

We compare ten PPM metrics (Table 2) including population growth rate, inertia, reactivity (herein referred to as ‘demographic properties’), elasticity (herein referred to as ‘selection potentials’) and vital rates of invasive plant populations in the invaded and native range to 1) determine if demographic processes change between ranges; and 2) identify the type of analyses that are most likely to reveal demographic or life history differences that facilitate invasion. On the basis of range specific differences identified previously (Hyatt and Araki, 2006, Parker et al., 2013, Hierro et al., 2013), and strong links between invasiveness and increased reproductive output (Burns et al., 2013, Moravcová et al., 2010, Mason et al., 2008, Burns, 2006, Jelbert et al., 2015) and associated proxies (Reichard, 1994, Cadotte and Lovett-Doust, 2001), it is predicted that in the invaded range invasive species will exhibit an enhanced ability to amplify in response to disturbance and rapid population growth. We predict that these demographic and life history differences will be revealed by analyses of transient dynamics because such analyses remove the assumption of SSS.

Materials & Methods

Demographic data were obtained from the COMPADRE Plant Matrix Database (COMPADRE 3.0.0) (Salguero-Gómez et al., 2014) and collected in the field (Table 1; Supporting Information at Appendix 1).

Table 1: Invasive Plant Species, Study Location and Data Source.

Species	Common Name	Native Study Range	Data Sources for Native Range	Invasive Study Range	Data Sources for the Invasive Range
Alliaria petiolata	Garlic mustard	Cornwall, UK	Jelbert (2014) unpublished	Michigan, USA	Evans et al. (2012)
Carduus nutans	Musk thistle	France	Jongejans et al. (2008)	Australia/ New Zealand	Shea and Kelly (1998)
Cirsium vulgare	Spear thistle	UK	Bullock et al. (1994)	Australia	Forcella and Wood (1986)
Iris pseudacorus	Yellow flag iris	Cornwall, UK	Jelbert (2014) unpublished	Louisiana, USA	Pathikonda et al. (2009)
Lotus corniculatus	Birds-foot trefoil	Cornwall, UK	Jelbert (2014) unpublished	Missouri, USA	Emery et al. (1999)
Lythrum salicaria	Purple loosestrife	Cornwall, UK	Jelbert (2014) unpublished	Ontario, Canada	Lacroix (2004)
Polygonum perfoliatum	Mile-a-minute weed	Japan	Hyatt and Araki (2006)	Pennsylvania, USA	Hyatt and Araki (2006)

Data Collection:

The COMPADRE Plant Matrix Database (COMPADRE 3.0.0) (Salguero-Gómez et al., 2014) features >7000 stage-structured demographic models for almost 700 species of plant. Population status for each Population Projection Matrix (PPM) within the COMPADRE Plant Matrix Database was classified as 1) native, 2) invasive or 3) naturalised, non-invasive at the study location using the source literature for each study. Species were also assigned a global status as 1) invasive, 2) naturalised but non-invasive outside of the native range, or 3) restricted to the native range. Species status outside of the native range was determined using invasive species databases, and academic and Government publications following the methodology set out in Jelbert et al. (2015). We filtered COMPADRE to identify invasive species for which demographic data, collated in both the native and invaded range, was available, yielding six species represented by multiple PPM's. We then filtered these PPM's to exclude 1) matrices generated by pooling data from multiple sites; 2) matrices generated for populations reared in the laboratory, greenhouse or experimentally manipulated; and 3) matrices that were reducible and therefore non-ergodic (StottTownley et al., 2010). Reducible and non-ergodic matrices were identified using the R package '`popdemo`'. All PPMs where checked for the 'seed problem'(Caswell, 2001), whereby the seed or propagule stage class is incorrectly presumed to last one year before germination, and corrected as appropriate. The filtered dataset comprised 23 spatial populations (many of them replicated through time), representing only three plant species.

To yield additional species, we filtered COMPADRE to identify invasive species 1) for which demographic data was available in the invaded range; 2) that are also native to Cornwall, UK; 3) for which the available demographic data met our criteria as outlined above; and 4) for which the source literature provided a methodology that could be replicated in the native range. The filtered dataset comprised four invasive species for which, demographic data was subsequently collected in the native range (Cornwall, UK) (see Supporting Information). The combined data (PPMs constructed from demographic data collected in the native and invaded range) derived from the COMPADRE Plant Matrix Database (COMPADRE 3.0.0) and collated in the field, represented seven invasive plant species (Table 1).

Demographic data were collected at sites in Cornwall, UK. Germination trials and seed viability analysis were also performed, the latter in accordance with the International Seed Testing Association (2014) and Peters (2000), to determine seed survival and transition rate out of the seed bank. The methodology is presented as Supporting Information.

Population Projection Matrix (PPM): Construction

A PPM, comprising demographic data collated in the native range, was constructed for each of the four invasive species measured in the field. The PPM's were constructed using the methodology detailed in the source literature for the corresponding PPM's in the invaded range (Pathikonda et al., 2009, Emery et al., 1999, Lacroix, 2004, Evans et al., 2012). The R package '`popdemo`' was used to confirm PPMs to be non-negative, irreducible and ergodic (qualities required to accurately describe transition rates between life cycle stages), and therefore suitable for analyses.

Deviations from the published methodology are as follows: the entries for *L. corniculatus* within COMPADRE comprise three seasonal matrices; using the methodology set out in Emery et al. (1999) these were converted into one annual matrix. This methodology was replicated to produce a single annual matrix for the native range. It was not possible to replicate the invaded range PPMs for *L. salicaria* (Lacroix, 2004) in the native range because 1) seed bank survival was not recorded due to high germination rate and inability to recover seeds for seed viability analysis; 2) quiescent individuals were not recorded in year 1; and 3) because the 12th stage of the native range matrix was empty (no individuals meeting the criteria were recorded). To compensate a 10 stage matrix was constructed by removing two seed stages; values for quiescent individuals were taken from the invasive range PPM, and a small value of 0.001 was fed into the native range matrix. Lacroix (2004)'s matrices were not reducible and non-ergodic due to empty life stages, and were therefore not suitable for analysis. To overcome this problem, the two matrices created by Lacroix (2004) were combined to create a single matrix that was irreducible, ergodic and subsequently suitable for analysis. The entries for *P. perfoliatum* within COMPADRE comprise three seasonal matrices (Hyatt and Araki, 2006); matrix multiplication was used as set out in Emery et al. (1999) to convert these into three annual matrices; this methodology was replicated to produce a single annual matrix for the native range.

Population Projection Matrix (PPM): Calculating Demographic Metrics

The following metrics were calculated for each species in the native and invaded range: log(lambda) (λ), log(inertia) (ρ_{∞}), log(reactivity) (demographic properties), vital rates (stasis, progression and recruitment) and elasticity of lambda to vital rates (Table 2). Note that lambda, inertia and reactivity were heavily skewed and were therefore log transformed to achieve an additive scale.

Table 2: Definition of Metrics Analysed.

Metric	**Lay Definition**
Log(Lambda)	Stable population growth rate, achieved by a population that has settled to stable stage structure. Natural log of the dominant eigenvalue of the population projection matrix.
Upper bound log(Inertia)	Upper bound on long-term impact of transient dynamics following disturbance away from stable stage structure. Measures the log of the ratio of future population size relative to that achieved by a population at stable stage structure.
Lower bound log(Inertia)	Lower bound on long-term impact of transient dynamics following disturbance away from stable stage structure.
Log(Reactivity)	Population boom or bust achieved, relative to stable rate of increase, in the first timestep following demographic disturbance. Can be described using upper and lower bounds.
Logit(Stasis)	The proportion of individuals that survive but do not progress to the next stage within the lifecycle, with logit transformation relevant to proportion data.
Logit(Recruitment)	The rate of reproduction, germination and seedling establishment, with logit transformation.
Logit(Progression)	The proportion of individuals that both survive and make the transition to the next stage within the lifecycle (growth), with logit transformation.
Elasticity(Stasis)	The proportional rate of change in stable population growth rate, in response to proportional increase in stasis.
Elasticity(Recruitment)	The proportional rate of change in stable population growth rate, in response to proportional increase in recruitment.
Elasticity(Progression)	The proportional rate of change in stable population growth rate, in response to proportional increase in progression.

Caswell (2001); Stott et al., (2011)

The Perron-Frobenius theorem describes how the dynamics of a non-negative, irreducible, ergodic projection matrix arrive at a stable stage structure (SSS) (relative density of stages in the population) and a stable geometric rate of increase (Caswell, 2001) from any initial condition when rates of transition between life stages are constant and growth is unlimited. The stable rate of population increase (λ) is the dominant eigenvalue of a PPM and the SSS is the normalised, dominant right eigenvector (Caswell, 2001). For each PPM λ was calculated using the '`lambda`' function in the R package '`popdemo`'. The SSS was calculated using the function '`eigen`' in the R package '`popdemo`'.

Demographic inertia (ρ_∞), also referred to as the Stable Equivalent Ratio (Koons et al., 2007), measures the long-term impacts of transient dynamics caused by disturbance away from the SSS (Stott et al., 2012). Where a non-stable population structure, caused by a higher density of one life stage compared to another, exists the population will be larger or smaller than the population exhibiting a SSS. This is often described as a 'boom or bust' effect, whereby the population amplifies (more population growth than predicted by λ) or attenuates (less population growth than predicted by λ). Here we measure the upper and lower bounds on inertia for each matrix model to describe the potential for demographic amplification and demographic attenuation, respectively. The upper ($\bar{\rho}_\infty$) and lower ($\underline{\rho}_\infty$) bounds of inertia were calculated using the '`inertia`' function in the R package '`popdemo`'. Projection matrices are described as either "pre-reproductive" (recruitment is measured as fecundity multiplied by rates of germination and seedling survival), or "post-reproductive" (recruitment of seeds measured as adult survival multiplied by fecundity). Post-reproductive matrices often exhibit high values of recruitment, which inflate measures of demographic amplification. To compensate, we converted all post-reproductive matrices to pre-reproductive matrices.

Reactivity is a measure of population size in the short-term (first time-step), and was calculated using the '`reactivity`' function in the R package '`popdemo`'.

It was not possible to obtain survival, growth and fecundity values from each PPM sourced from the COMPADRE 3.0.0 Plant Matrix Database (Salguero-Gómez et al., 2014) because these values are not presented in the source literature and because survival and transition probabilities have been multiplied and cannot be disentangled. Instead we use the vital rates, stasis, recruitment and progression as proxies for survival, fecundity and growth. Stasis describes the proportion of individuals that survive but do not progress to the next stage within the lifecycle. Progression describes the proportion of individuals that both survive and make the transition to the next stage within the lifecycle (growth). Recruitment describes the rate of reproduction, germination and seedling establishment. An abundance weighted average between the population structure of the PPM and the SSS was used to calculate the average demographic rate for stasis, recruitment and progression for each species in the native and invaded range. Average vital rates were not normally distributed therefore recruitment was logged, and stasis and progression were logit transformed because both are bound by zero.

We used elasticity analysis to explore the effect of stasis, recruitment and progression on population growth rate (Franco and Silvertown, 2004). Elasticities of matrix transition rates sum to one. The sum of elasticities of lambda for each vital rate is used to determine their relative influence on lambda, and whether this differs between the native and invaded range. For each population elasticity matrices were calculated using the function ‘`elas`’ in the R package ‘`popdemo`’.

Data analysis

Ten metrics were calculated for each species in the native and invaded range: log(λ), upper ($\bar{\rho}_\infty$) and lower ($\underline{\rho}_\infty$) bounds of log(inertia), log(reactivity) (demographic properties); vital rates (logit stasis, logit recruitment and logit progression) and elasticity of lambda to vital rates (stasis, recruitment and progression) (selection potentials). Multiple populations, and therefore PPMs were available for some species, and within a species, the number of PPMs generated from data collated in the native and invaded range was not the same. An average of metrics for each species was therefore calculated to mitigate the irregularity of PPMs, resulting in metric averages for seven species in both the native and invaded range. A pairwise t test was conducted for each of the ten metrics. Multiple testing in this manner has potential to exaggerate Type I errors (i.e. false positive outcomes). Principal Component Analysis (PCA) was therefore performed to reduce the dimensionality of the data into dominant axes, which explain most of the variation.

The PCA scores were used to distinguish the effects of range (native or invaded) on the magnitude of metrics, the *a priori* one-way hypothesis being that plants in the invaded range will show greater magnitudes. A one tailed t test was used to determine whether species position on the selected PCA axis(es) differ(s) between the invaded range and native range. In accordance with Kaiser's Criterion (Costello and Osborne, 2005) PCA axes were only retained for analysis where their associated eigenvalue was ≥ 1. We use the `evplot` in R to calculate eigenvalues for each PCA axis. Initially all PPM metrics were included within the PCA. Due to large variation amongst metrics, with potential to obscure important relationships, PCA was subsequently performed separately for 1) vital rates (stasis, recruitment and progression); 2) selection potentials (elasticity of λ to stasis, recruitment and progression); and 3) demographic properties (inertia, λ and reactivity).

All analyses were performed using RStudio version 1.1.383 (2015).

Results

Pairwise t-test of metrics

We find no significant difference in log(λ) between the invaded and native range (t_6 = 0.27626, p-value = 0.791), though on average, across the seven species, log(λ) was higher in the invaded range (Figure 1a; Table 3). Considerable variation in log(λ) in the native range, driven by a small number of extreme values, may have concealed a significant difference between ranges.

The upper bounds of log(inertia) ($\bar{\rho}_\infty$) was significantly larger in the invaded range (t_6 = 3.3824, p-value = 0.015; Figure 1b; Table 3). We find no significant difference in the lower bounds of log $\underline{\rho}_\infty$ between the invaded and native range (t_6 = -0.3178, p-value = 0.761; Table 3); this metric displayed considerable variation.

We find log(reactivity) to be significantly lower in native range; in the invaded range the maximum response of population growth to disturbance is significantly higher (t_6 = 2.9284, p-value = 0.026; Figure 1c; Table 3).

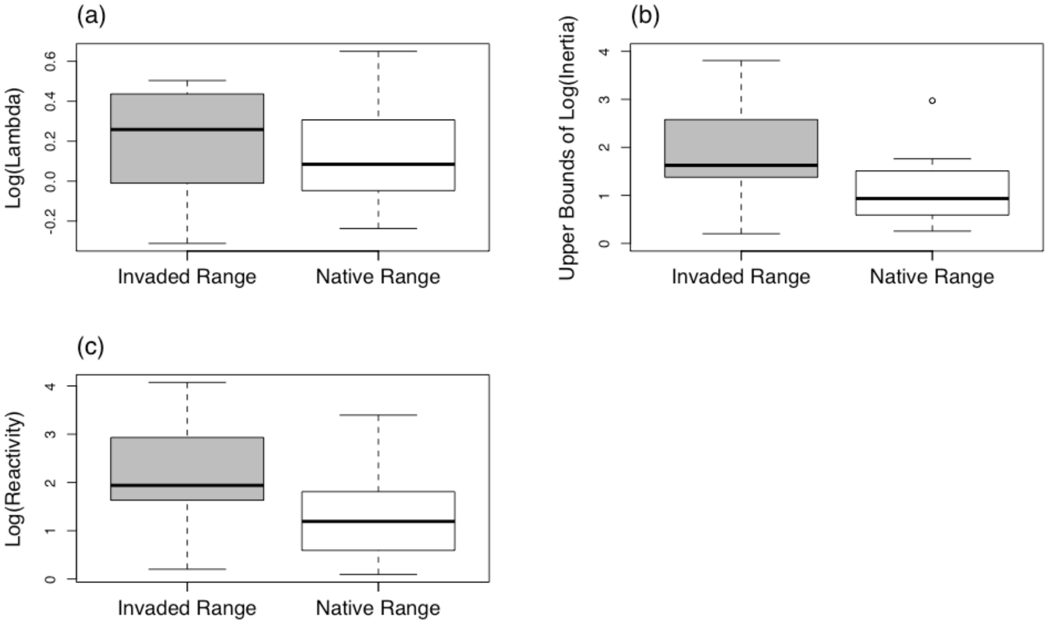


Figure 1: Boxplot showing the distribution of variance of a) log(lambda); b) the upper bound of log(Inertia); and c) log(reactivity) for invasive plant species (n = 7) in the native and invaded range. The medium is shown as the thick, black, dividing line; the upper and lower quartiles as the upper and lower edge of rectangles; the maximum and minimum values as the outer bars; and the outliers as points.

The vital rates: logit(stasis), logit(progression) and logit(recruitment), were found not to be significantly different between the native and invaded range (Table 3). Vital rates, notably stasis, exhibited the largest confidence intervals; variation in these rates may have concealed a significant difference between ranges. Finally, we find elasticity of λ to the vital rates, referred to as E(Stasis), E(Progression) and E(Recruitment), not to differ significantly between the native and invaded range (Table 3) but to reveal some anomalies. Population growth rate of both *A. petiolata* and *I. pseudacorus* appear to be strongly influenced by progression in the native range but more heavily influenced by stasis in the invaded range. Population growth rate of *L. salicaria* is highly elastic to recruitment and stasis in the native range but switches to become strongly influenced by progression and recruitment in the invaded range (Figure 2). Similarly *L. corniculatus* is strongly influenced by stasis in the native range but is more heavily influenced by recruitment in the invaded range (Figure 2).

Table 3: Pairwise t test range comparison of metrics – test statistics.

Metric	**Mean of differences**	**t-value**	**Degrees of freedom (*df*)**	**p-value**
Log(Lambda)	0.041	0.27626	6	0.791
Upper bound log(Inertia)	0.741	3.3824	6	0.015*
Lower bound log(Inertia)	-0.196	-0.31782	6	0.761
Log(Reactivity)	0.837	2.9284	6	0.026*
Logit(Stasis)	-0.790	-0.49185	6	0.640
Logit(Recruitment)	0.454	1.0874	6	0.319
Logit(Progression)	-0.370	-0.3702555	6	0.670
E(Stasis)	0.129	0.87446	6	0.416
E(Recruitment)	0.043	0.34879	6	0.739
E(Progression)	-0.085	-0.92088	6	0.392

* represents a significant result

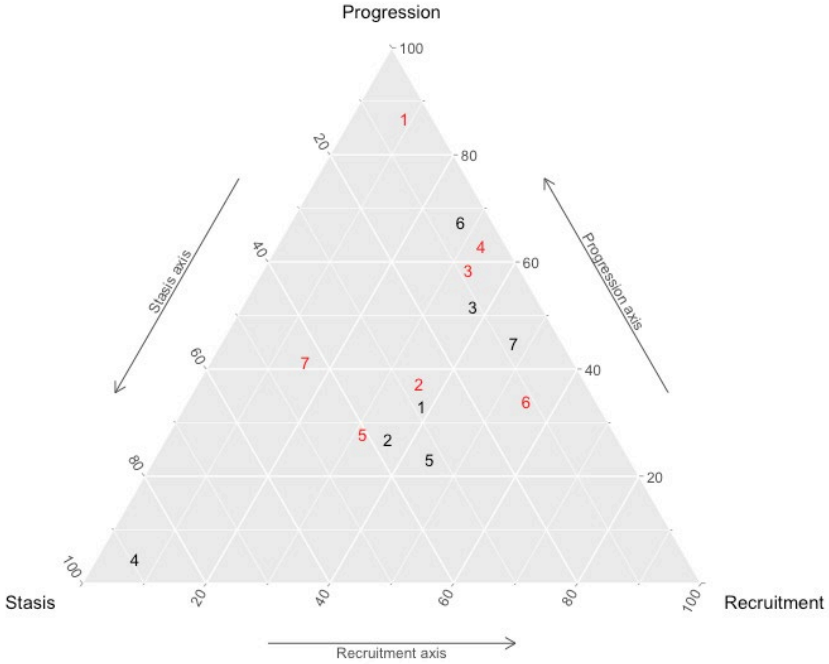


Figure 2: Ternary plot showing the relative influence of the vital rates: stasis, recruitment and progression, on lambda (elasticities) for each invasive species (n = 7) in the native (black numbers) and invaded (red numbers) range. Our species: *Alliaria petiolata*, *Carduus nutans*, *Cirsium vulgare*, *Iris pseudacorus*, *Polygonum perfoliatum, Lythrum salicaria* and *Lotus corniculatus* are represented by the numbers 1 – 7 respectively.

Principal Component Analysis

Principal Component Analysis (PCA) was performed to reduce the dimensionality of the data into dominant axes, which explain most of the variation. Initially PCA was performed for all PPM metrics (vital rates, selection potentials and demographic properties). In accordance with Kaiser's Criterion (Costello and Osborne, 2005) we retain PCA axes 1 – 4 because the eigenvalues are ≥ 1. In combination these PCA axes explain 86% of the variation. The first principal component axis (PCA1 All Metrics) explains 37% of the variation (Figure 3). On the PCA1 All Metrics axis, the lower bound of log inertia ($\underline{\rho}_\infty$) (the propensity of a population to 'attenuate' in response to disturbance) is correlated with the elasticity of stasis on population growth rate (Stasis Elasticity) and the vital rate 'stasis', and sits at the negative end of the axis, whilst the opposite, positive end of the axis represents contribution from the 'amplification' traits: log $\bar{\rho}_\infty$, log(reactivity) and a log(recruitment) (Figure 3). The second principal component axis (PCA2 All Metrics), which explains 23% of the variation, indicates population growth to be correlated with either elasticity of progression (Progression Elasticity) or stasis (Stasis Elasticity) on population growth, but not both (Figure 3). Of the seven invasive species, *L. salicaria* and *I. pseudacorus* are most strongly influenced by PCA2.

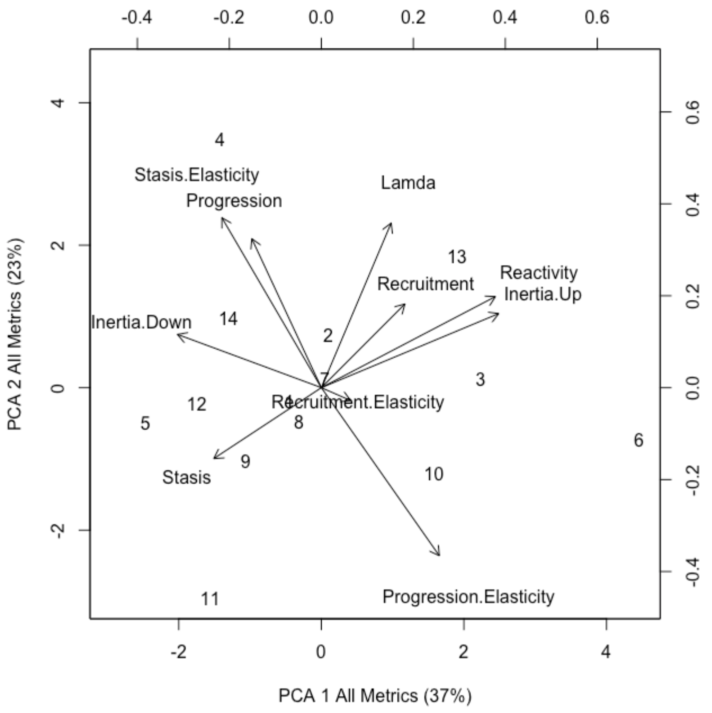


Figure 3: Position of all demographic metrics for the native and invaded range on the PCA axes. Populations exhibit a faster life cycle in the invaded range if positioned on the positive side of the PCA1 axis relative to their conspecific in the native range. *Alliaria petiolata*, *Carduus nutans*, *Cirsium vulgare*, *Iris pseudacorus*, *Polygonum perfoliatum, Lythrum salicaria* and *Lotus corniculatus* are represented by the numbers 1 – 7 in the invaded range and 8 – 14 in the native range respectively.

A one tailed t test was used to determine if invasive species exhibit a faster life history (sit higher on the positive end of the PCA1 All Metrics axis) when in the invaded range. We find that invasive plants do not exhibit a significantly higher PCA1 score than plants in the native range (t_6=2.1618, P = 0.066; Figure 3). However, of the 7 study species, 5 exhibit a higher PCA1 scores in the invaded range, the anomalies being *P. perfoliatum* and *A. petiolata*, which exhibit a higher PCA1 score in the native range. Similarly, we find that invasive plants do not exhibit a significantly different PCA2 score between ranges (t_6=0.81434, P = 0.223; Figure 3), PCA3 score (t_6=-0.78285, P = 0.768) or PCA4 score (t_6=0.49762, P = 0.318) for all metrics. We previously showed that in the invaded range invasive plants exhibit significantly higher reactivity and upper bound of inertia: these are demographic properties that may be masked by high variation amongst vital rates and selection potentials (elasticities) when lumped into a single PCA. We have therefore undertaken separate PCA for demographic properties, vital rates and selection potentials.

For demographic properties we find that invasive plants exhibit a significantly higher PCA1 score in the invaded range (t_6=2.0176, P = 0.045; Figure 4), representing higher values of the 'amplification' traits: log $\bar{\rho}_\infty$ and log(reactivity), in the invaded range. In accordance with Kaiser's Criterion (Costello and Osborne, 2005) we only retain the PCA1 axis because the eigenvalues of subsequent PCA axes are < 1.

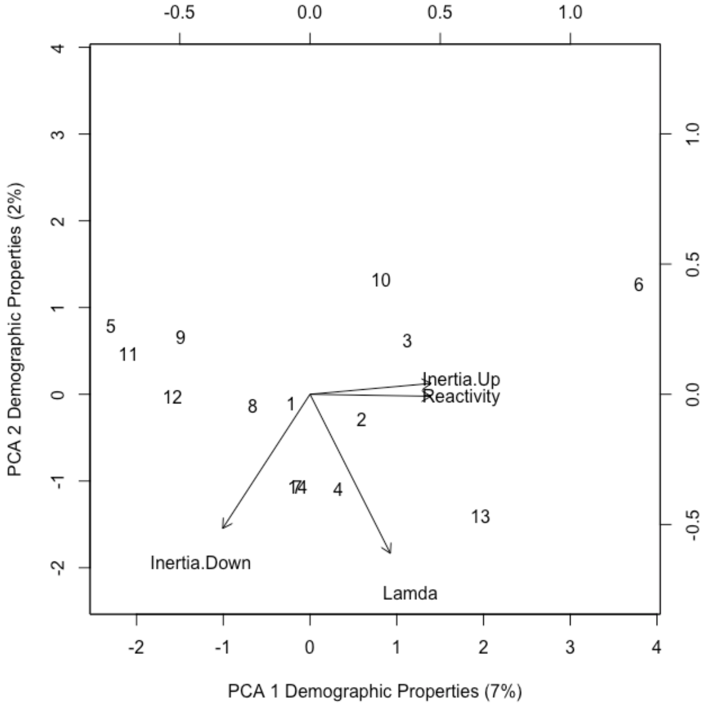


Figure 4: Position of demographic properties for the native and invaded range on the PCA axes. Populations exhibit a higher population growth, reactivity and the upper bound of inertia in the invaded range if positioned on the positive side of the PCA1 axis relative to their conspecific in the native range. *Alliaria petiolata*, *Carduus nutans*, *Cirsium vulgare*, *Iris pseudacorus*, *Polygonum perfoliatum, Lythrum salicaria* and *Lotus corniculatus* are represented by the numbers 1 – 7 in the invaded range and 8 – 14 in the native range respectively.

For vital rates we find that invasive plants do not exhibit a significantly different PCA1 score (t_6= -0.70194, P = 0.746; Figure 5), or PCA2 score (t_6= 1.0825, P = 0.160; Figure 5) between ranges.

For selection potentials we find that invasive plants do not exhibit a significantly different PCA1 score (t_6= -0.79612, P = 0.772; Figure 6) between ranges. In accordance with Kaiser's Criterion we only retain the PCA1 axis because the eigenvalues of subsequent PCA axes are < 1.

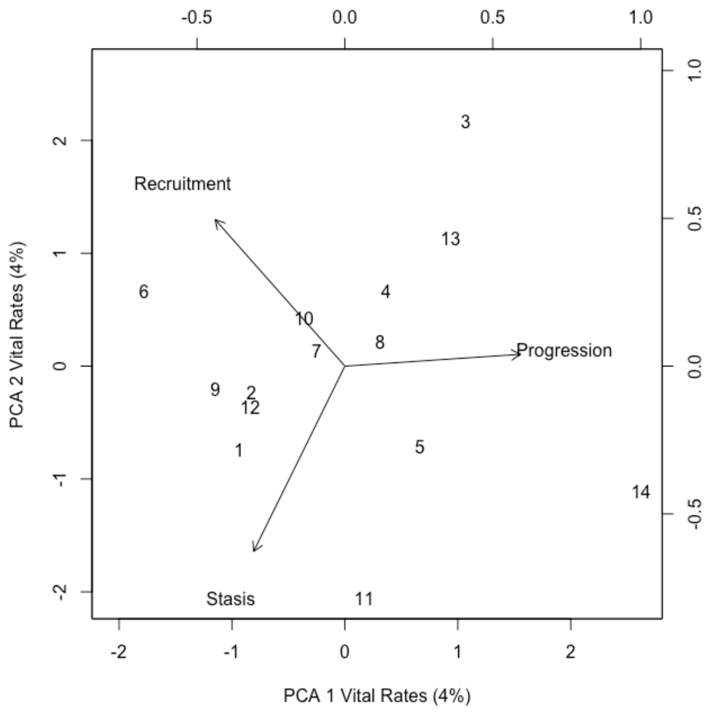


Figure 5: Position of vital rates for native and invaded range populations on the PCA axes. *Alliaria petiolata*, *Carduus nutans*, *Cirsium vulgare*, *Iris pseudacorus*, *Polygonum perfoliatum, Lythrum salicaria* and *Lotus corniculatus* are represented by the numbers 1 – 7 in the invaded range and 8 – 14 in the native range respectively.

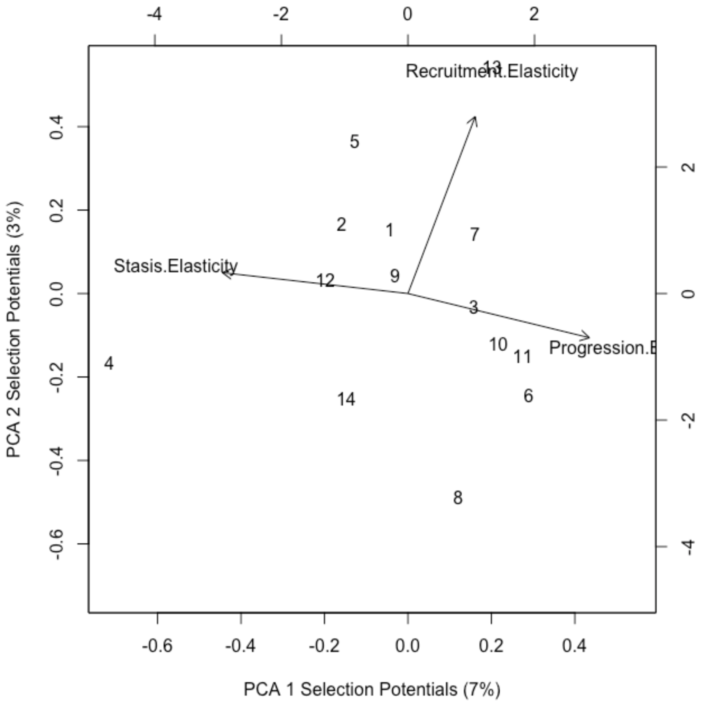


Figure 6: Position of selection potentials for native and invaded range populations on the PCA axes. *Alliaria petiolata*, *Carduus nutans*, *Cirsium vulgare*, *Iris pseudacorus*, *Polygonum perfoliatum, Lythrum salicaria* and *Lotus corniculatus* are represented by the numbers 1 – 7 in the invaded range and 8 – 14 in the native range respectively.

Discussion

An ability to predict which species will become invasive is required to contain and mitigate the impact of existing invasive populations, and to prevent further harmful species introductions. Here we compare the demography of seven invasive plant species between the native and invaded range to determine if demographic processes change between ranges, and to identify the analyses most likely to reveal demographic or life history differences that facilitate invasion. Specifically, we tested whether a) population growth rate (λ); b) inertia; c) reactivity (demographic properties); d) vital rates; and e) elasticity of λ to changes in vital rates (selection potentials), differ between the invaded and native range. We also tested if invasive plant species in the invaded range show greater magnitudes of these metrics when the dimensionality of the data is reduced into dominant Principal Component axes. We predicted that in the invaded range invasive species will exhibit an enhanced ability to amplify in response to disturbance and rapid population growth, and that these differences will be revealed by analyses that do not assume stable stage structure (SSS).

We find that the properties of invasiveness are revealed by demographic properties: invasive plants in the invaded range exhibit a significantly higher PCA1 score than conspecific populations in the native range when PCA is restricted to demographic properties only; invading populations are positioned higher on the positive end of the axis, which represents the indices of transient dynamics and 'amplification' traits: log $\bar{\rho}_\infty$ and log(reactivity). Similarly, conspecific range comparison of individual metrics revealed reactivity and the upper bound of inertia ($\bar{\rho}_\infty$) (maximum ability of population to amplify or boom in response to disturbance) to be significantly higher in the invaded range. Principal Component Analysis of all metrics (demographic properties, vital rates and selection potentials) revealed no such relationship, as did PCA when restricted to vital rates or selection potentials. Analysis of SSD-weighted mean vital rates and elasticities assume the population to be at SSS (Caswell, 2001) but invasiveness is typically a property of disturbed environments where populations do not achieve a SSS. We predicted that such analyses are unlikely to be sufficiently sensitive to detect range specific differences of invasive plant populations, and our results support this hypothesis. Transient measures of demographic properties do not assume a SSS and instead measure the impact of not being at SSS (Koons et al., 2007, Stott et al., 2011). In support of our hypothesis, our results indicate that analyses of transient dynamics are better suited to identify differences amongst invading plant populations, which are assumed not to be at SSS. When demographic properties, vital rates and selection potentials are lumped into a single PCA, the assumption of SSS for vital rates and selection potentials potentially obscures range specific differences amongst demographic properties.

There were two anomalies amongst our invasive species: *P. perfoliatum* and *A. petiolata* did not exhibit higher reactivity and the upper bound of inertia ($\bar{\rho}_\infty$) in the invaded range. Possible explanations include biogeography and variation in the mechanism of invasion. *P. perfoliatum*, a vine, is native to Japan (Hyatt and Araki, 2006) whilst the other invasive species in our study are native to Europe (Pathikonda et al., 2009, Emery et al., 1999, Lacroix, 2004, Evans et al., 2012). In the native range periodic fluvial flooding causes seedling and adult survivorship to be considerably lower than in the invaded range where flooding events are rare (Hyatt and Araki, 2006). Population growth in the native range is slightly more dependent on progression, whilst population growth in the invaded range is marginally more dependent on recruitment and stasis but these differences are minor in extent. In the invaded range *P. perfoliatum* outcompetes native species by attaining a large size that inhibits the photosynthetic ability of its neighbours. High rates of recruitment and progression may not be necessary for *P. perfoliatum* to establish and spread; this is consistent with Hyatt and Araki (2006)'s observation that invading populations are equally elastic to (affected by changes in) germination, fecundity, seed bank and survival. In the native range population growth of *A. petiolata* is driven by progression but in the invaded range becomes largely dependent on adult survivorship. The impact of recruitment on population growth is unaffected by range.

Of the individual metrics compared between ranges, we find the upper bound of inertia to be significantly higher in the invaded range. The size of populations disturbed away from SSS will amplify or attenuate in the short-term, before arriving at the stable rate of increase (or decline). Demographic inertia measures the long-term impact of this transient dynamic whereby non-stable populations will always be larger or smaller than a population initiated at SSS (Koons et al., 2007). The *a priori* hypothesis is supported, an invading population could attain a population size larger than a native conspecific population. This finding supports mathematical simulations, which have illustrated how high population inertia could theoretically explain invasion success, and be an adaptation to invasion (Guiver et al., 2015). Reactivity is similar to inertia, and describes maximum amplification encountered following disturbance but unlike inertia is restricted to the first timestep (Neubert and Caswell, 1997, StottFranco et al., 2010). We find reactivity 'the magnitude of the boom' to be significantly higher in the invaded range indicating that freed from the constraints of the native range, plants can better exploit favourable conditions.

Unexpectedly, there was no statistically significant difference in projected stable population growth rate between the native and invaded range. This is consistent with our finding that invasive plants in the invaded range exhibit higher magnitudes of reactivity and the upper bound of inertia (amplification traits), and previous findings that greater long-term population growth and increased population viability (proxies of invasiveness) are dependent on the presence of 'amplificatory traits' (Iles et al., 2016, Ramula et al., 2008, Burns et al., 2013).

The vital rates and elasticity of lambda to demographic rates were found not to be significantly different between the native and invaded range. There were however, some notable anomalies: *Iris pseudacorus* switched from being highly elastic to progression and recruitment in the native range to being highly elastic to stasis in the invaded range. A possible explanation pertains to vigorous growth of *I. pseudacorus* populations through rhizomes (Pathikonda et al., 2009). In this scenario it is intuitive that population growth will not be dependent on increased seed production and is perhaps more dependent on adult survivorship. *Lythrum salicaria* exhibits the reverse relationship, and shifts from being highly elastic to progression in the native range to being highly elastic to recruitment in the invaded range. An average mature *L. salicaria* plant produces 2.7 million seeds per annum (Thompson et al., 1987). Unlike *I. pseudacorus*, reproduction and spread rate of *L. salicaria* is dependent on seed production.

In this study we show that the demographic properties, upper bound of inertia and reactivity, differ between ranges whilst vital rates and selection potentials do not. Invasive plant species exhibit a greater propensity to 'amplify' or 'boom' in response to disturbance in the invaded range. Large amplification is a characteristic of plant life histories with high reproductive output (Stott et al., 2011). Freed from the constraints of the native range, invading plant populations exhibit a higher population growth rate in response to disturbance, and an elevated magnitude of reactivity. Species exhibiting high amplification can evolve more quickly to changing environmental conditions, are more likely to replace variation lost as a result of genetic bottlenecks (i.e. those occurring following introduction to a new environment) and are therefore less vulnerable to demographic stochasticity (Rice and Emery, 2003).

We find that the properties of invasiveness are revealed by demographic properties as opposed to vital rates and selection potentials. This we attribute to the appropriateness of the measure. Invasiveness is often a property of disturbed environments (D'Antonio, Dudley & Mack 1999; Marvier, Kareiva & Neubert 2004) where populations do not achieve a SSS. Unlike stable population growth rate, vital rates and elasticities, which assume a SSS, transient measures of demographic properties do not and instead measure the impact of not being at SSS (Koons et al., 2007, Stott et al., 2011). Analysis of transient demographic properties is therefore more likely to detect range specific differences in demographic and life history traits amongst invasive populations. We suggest that demographic amplification, caused by subtle changes to vital rates across the entire life cycle, is an important promotor of invasiveness.

It is important to note that our study comprised only seven species, six of which are native to Europe. The relatively low sample size, coupled with large variation amongst vital rates and selection potentials, and the restricted geography of study species, reduces the proficiency with which our results can be used to predict global patterns of invasive plant demography. Our results could be specific to the study species and locations. It is however, important to recognise that extensive demographic data is contained within a single PPM. Population Projection Matrices derived from the COMPADRE Plant Matrix Database (Salguero-Gómez et al., 2014) represent a minimum of two years intensive monitoring; and multiple PPMs derived from distinct populations, are available for some of our study species. Furthermore, PPMs derived from field data collected in Cornwall, UK were constructed using a minimum of 92 plants and a maximum 290 plants.

Future research should test whether our findings are true for a greater number of species that are representative of a variety of plant life forms, reproductive strategies and a broad geographical range. Future research would benefit from including some of the most problematic invasive species such as *Fallopia japonica*, *Eichhornia crassipes* and *Acacia spp*., (Lowe et al., 2000) which are absent from this study.

Author Contributions

The study was conceived by KJ & DH. Data were collected by KJ and were analyzed by KJ, SDK & DH. The manuscript was written by KJ, SDK & DH.

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Supporting Information

Data Collection: Field

Demographic data from the native range was collected at sites in Cornwall, UK. Sites supporting each population were identified using the ERICA Database held by Dr. Colin French and were selected as described in Jelbert et al. (2015). To minimize the effect of environmental variables on demographic parameters, study sites in the native range were selected to emulate habitat at study locations in the invaded range as described in the source literature (Pathikonda et al., 2009, Emery et al., 1999, Lacroix, 2004, Evans et al., 2012).

Permanently marked, geo-referenced quadrats (mean = 10) were installed at each site as described in Jelbert et al. (2015). Quadrat size was determined by the species' area-weighted density (range: 0.5 x 0.5m - 1m x 1m) (Jelbert et al., 2015). Individual plants within each quadrat were repeatedly monitored between May and October 2013, encompassing late spring, summer and autumn (to determine fecundity), and once between May and October 2014 (to determine recruitment, survival, growth and retrogression transitions). In accordance with the published PPMs derived from the invaded range (Pathikonda et al., 2009, Emery et al., 1999, Lacroix, 2004, Evans et al., 2012), we consider an individual to be an entire plant or, for clonal rhizomatous species, a ramet (an individual belonging to a clonal group of genetically identical individuals) and use the term 'plant(s)' to refer to these individuals. We recorded the life-stage (i.e. seedling, vegetative, reproductive etc.) of all individuals within each quadrat, and if present, the number of seed capsules or racemes per plant from which we calculated fecundity (Jelbert et al., 2015). We also recorded parameters of size (basal stem diameter, rosette diameter and rosette perpendicular diameter) during each visit. Germination and seed viability analysis were conducted to determine seed survival and transition rate out of the seed bank as described at Appendix 1.

Data Collection: Germination Trial

Germination trials were conducted to determine seed survival and transition rate out of the seed bank. All species are likely to require a period of vernalization prior to germination. To replicate minimum winter ground temperatures in the native range, seed collected and air dried as described in Jelbert et al. (2015), was stored at 5°C between collection in Summer 2013, and sowing in January 2014. Field germination trials following the methodology set out in the original published source of the invaded range PPM (where available) were unsuccessful due to perforation of the muslin cloth seed bags. Germination trials were instead conducted in a cold frame located a maximum of 15 miles from each sample population; photoperiod was therefore consistent with the photoperiod experienced by wild plants. Seed (n = 300) was sown at a depth of 3mm in a sterile / seed free substrate. Substrate was selected to replicate soil type at each site. This comprised 100% seed compost for *Lotus corniculatus*, *Iris pseudacorus*, *Lythrum salicaria* and *Alliaria petiolata*, which typically occur in neutral and nutrient rich soils.

Sown seeds were watered (300ml per tray) and the number of germinated seeds counted and removed, every two days between sowing in January and June 2014 inclusive. In July 2014 seeds that failed to germinate were recovered. To estimate seed survival after one year in the seed bank, seeds were subjected to seed viability analysis.

Data Collection: Seed Viability Analysis

Tetrazolium staining was used to estimate seed survival after one year in the seed bank. Seed was submerged in a 1% solution of 2,3,5-triphenyl tetrazolium chloride (1g 2,3,5-triphenyl tetrazolium chloride in a 100ml buffer mix as described below) for a species specific length of exposure at 30°C in accordance with the International Rules for Seed Testing (International Seed Testing Association, 2014). A buffer, comprising two parts solution 1 (0.9078g KH_2PO_4 Monopotassium phosphate in 100ml of distilled water) and three parts solution 2 (0.9472g Na_2HPO_4 Disodium hydrogen phosphate in 100ml of distilled water), was used to achieve the desired pH (6.5 – 7.5). Seed viability was determined by the staining pattern in accordance with the International Rules for Seed Testing (International Seed Testing Association, 2014) and Peters (2000).

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Chapter 6:

Discussion

Our Approach to Invasive Species Research

The many adverse impacts of invasive species and the large costs of curtailing damages are widely documented (Butchart et al., 2010, Paini et al., 2016, Pimentel et al., 2005, Williams et al., 2010). The gravity of invasive species research is perhaps best illustrated by the existence of academic journals with sole focus on invasion biology. Central to the containment and control of invasive plant species is a means to predict which species will become invasive, and an understanding of the mechanisms of invasion. Using field experiments and meta-analyses we have presented phenotypic and demographic attributes of invasive plant species that can be utilised to predict which species will likely become invasive following introduction outside of the native range. We have shown that invasive species are both larger and constitutively more fecund than their non-invasive, sympatric relatives in the native range (Chapter 2; Jelbert et al. (2015)). We also found that invasive species exhibit higher reproductive investment (fecundity x seed mass) suggesting that invasive plants escape the typical trade-offs of competition and colonization, or of fecundity and tolerance, and exhibit higher fecundity without a resultant decrease in seed mass (Chapter 3). Using a meta-analysis, we disentangled the impact of range (native or naturalised), phylogeny and global plant status to demonstrate that invasive plant species exhibit greater potential for demographic amplification ($\bar{\rho}_{\infty}$) than non-invasive species and that this relationship shows phylogenetic pattern (Chapter 4). We also found that stable rates of population growth (λ) were greater in the introduced range irrespective of invasive status, and that this relationship lacks phylogenetic constraints (Chapter 4). Finally, we have shown that demographic properties changed between the native and invaded range; invasive plants exhibited greater propensity to amplify in response to disturbance in the invaded range, than conspecific native populations (Chapter 5).

This thesis has been structured in the order that each data chapter was conceived. Chapter 2 (the first of four data chapters; Jelbert et al. (2015)) compared plant size between invasive and non-invasive sympatric congeners, then controlled for plant size to determine if invasive plants exhibited higher fecundity, and higher probability of seed-set, than non-invasive plants. Plant size is a fundamental consideration because within a species, larger individuals characteristically exhibit higher fecundity (Weiner et al., 2009) and because large size, in varying forms (Schlaepfer et al., 2010, van Kleunen et al., 2011, Pyšek and Richardson, 2007, Grotkopp et al., 2002), is a correlate of invasiveness. Invasive plant species might be invasive because they are larger (and therefore more fecund) or because they are constitutively more fecund (i.e. higher fecundity per-unit-size) than their non-invasive counterparts. We found that invasives are both larger and constitutively more fecund (Jelbert et al., 2015). Chapter 2 also considered the effect of population structure on fecundity. This is important because a species with a population structure comprising few reproductive individuals may perform poorly in comparison to a species with a population comprising many reproductive individuals, even if the poorly performing species exhibits higher individual fecundity. We found no evidence that invasive species attempted to make seed more frequently than their sympatric, non-invading relatives. Finally, and perhaps the most unique aspect of Chapter 2, which is carried forward throughout this thesis, is the recognition that study range (native or naturalised) affects the questions that can be asked. It is well established that environmental variation contributes to variation in demographic parameters and predictions (Buckley et al., 2010, Morris and Doak, 2005), and that seed size (Hierro et al., 2013, Graebner et al., 2012, Buckley et al., 2003) and fecundity (Parker et al., 2013) have been observed to increase in the invaded range. We therefore chose to study our invasive and non-invasive species in the native range so not to conflate predictors of invasiveness with changes that might occur during invasion. We concluded that demographic parameters associated with invasiveness in the invaded range might be poor predictors of invasiveness, when the goal is to identify potential invasive species before they are introduced.

Chapter 2 (Jelbert et al., 2015) lead to our observation of the seed mass – fecundity paradox in the ecology of invasive species, which we address in Chapter 3. We noted that a number of studies identified small seed mass to be a correlate of invasiveness (Hamilton et al., 2005, Grotkopp et al., 2002, Rejmánek and Richardson, 1996, Graebner et al., 2012), while some found no association (Schlaepfer et al., 2010, van Kleunen and Johnson, 2007, Dawson et al., 2011, Mihulka et al., 2003) and others found that invasive species exhibited larger seed mass than their co-occurring native congeners (Daws et al., 2007); and non-invasive species (Lake and Leishman, 2004) in the introduced range. This we found intriguing because small seeded species are typically more fecund than larger seeded species (Turnbull et al., 1999, Rees and Westoby, 1997, Coomes and Grubb, 2003), and high fecundity has been consistently correlated with invasiveness (Jelbert et al., 2015, Burns et al., 2013, Burns, 2006, Mason et al., 2008, Moravcová et al., 2010). Theory would therefore predict small seed mass to be consistently correlated with invasiveness but it is not (Schlaepfer et al., 2010, van Kleunen and Johnson, 2007, Dawson et al., 2011, Mihulka et al., 2003). We hypothesized that this was because invasive plant species are more fecund for a given seed mass than non-invasives, and using the same wild populations as Jelbert et al. (2015) (Chapter 2) we tested this hypothesis, which we found to be supported.

In Chapters 2 and 3 we chose to compare invasive and non-invasive, sympatric congener pairs in order to account for the effect of phylogeny and environment. This was felt to be important because seed size and seed production are regulated by the structure of reproductive organs, which are in turn shaped by evolutionary history (Dani & Kodandaramaiah, 2017). In Chapter 4 we show that invasive plant species exhibit greater potential for demographic amplification, which is correlated with per capita recruitment per lifestage (a proxy for fecundity), and that this relationship shows phylogenetic patterns. Furthermore, the environment contributes to variation in demographic parameters and predictions (Buckley et al., 2010, Morris and Doak, 2005). It was felt that failure to account for phylogenic relatedness and environment could conceal or inflate any identified invasiveness trait(s) or syndrome. However, our sympatric, congener pair criteria restricted our sample size in Chapters 2 and 3 to only five pairs. An alternative approach would be to compare sympatric invasive and non-invasive un-related species and/ or to compare the invasive species' with multiple non-invasive species. This approach would likely yield a greater sample size, which could be further increased by comparing unrelated species that do not occur sympatrically. A possible benefit of increasing the sample size in this manner is the potential to account for the effect of time since introduction and propagule pressure (previously identified correlates of invasiveness; Goodwin et al., (1999), Reichard and Hamilton (1997), Herron et al., (2007), Richardson and Pyšek, (2006)). The 'perfect' field experiment might compare a greater number of sympatric, congener pairs that are representative of the global diversity of plants, in both their native and invaded range so to account for the effect of phylogeny and environment, whilst also accounting for the effect of time since introduction, propagule pressure and study location.

Chapter 2 (Jelbert et al., 2015), and previous work by Stott et al. (2010) and Stott et al. (2012) influenced the direction of our invasive versus non-invasive, comparative demographic meta-analysis (Chapter 4). In Chapter 2 (Jelbert et al., 2015) we found that invasive plants are larger and more fecund than non-invasive plant species with which they sympatrically occur in the native range. Stott et al. (2010) observed that highly fecund species have a superior ability to amplify in response to exogenous disturbances, and in a comparative analysis of the transient population dynamics of 108 plant species (Stott et al., 2012) identified that populations projected to grow faster in the long-term exhibit larger magnitudes of amplification and attenuation than populations growing more slowly or declining. We speculated that the comparatively high fecundity of invasive species compared to non-invasive species signals their greater ability to amplify in the short-term in response to demographic disturbances, permitting both rapid colonisation and long-term population growth.

In Chapter 4 we compare inertia (ρ_∞) (transient amplification and attenuation) and the stable rate of population increase ($\lambda_{\max}$) of invasive and non-invasive plants, whilst simultaneously controlling for phylogeny, range (native or naturalised) and global invasion status. We found that invasive plant species exhibited greater potential for demographic amplification ($\bar{\rho}_\infty$) than non-invasive species irrespective of range and that this relationship shows phylogenetic patterns; we also show that amplification correlated positively with per capita recruitment per lifestage (a proxy for fecundity, which was not available for many species). This indicates that high rates of recruitment drive high amplification, and that amplification is a species-specific trait that influences recovery from demographic disturbance and which differs between invasive and non-invasive plant species. Irrespective of invasive status, the stable rates of population growth (λ) were greater in the naturalised range than in the native range, indicating that stable population growth rate is heavily influenced by exogenous conditions, and unlike reproductive ability, is not a useful predictor of potential invasiveness.

Chapters 2 – 4 focused on comparing phenotypic and demographic traits of invasive and non-invasive species, to reveal reproductive capacity to be a useful predictor of potential invasiveness. Yet, these Chapters did not provide an insight into how demographic processes might change following introduction to a new environment. Chapter 5 addressed this by comparing ten metrics of seven invasive plant species, in both the invaded and native range. We found that in contrast to conspecific populations in the native range, invasive plants in the invaded range exhibited greater capacity to amplify in response to disturbance, and crucially that the properties of invasiveness were revealed by demographic properties and not vital rates or selection potentials (elasticities). We attributed this to the appropriateness of the measure. Vital rates and elasticities assume a Stable Stage Structure (SSS) (Caswell, 2001), which is unlikely to be achieved by invasive populations because invasiveness is often a property of disturbed environments (Marvier et al., 2004). Transient measures of demographic properties do not assume a SSS and instead measure the impact of not being at SSS (Stott et al., 2011), an approach better suited for detecting demographic and life history differences amongst invasive populations that are unlikely to achieve SSS. Chapter 5 echoes the findings of Chapter 4 and concludes that demographic amplification is a promotor of invasiveness. We do not consider there to be a conflict between the findings of Chapters 4 and 5 because Chapter 4 compares demographic performance between species, whilst Chapter 5 compares range specific performance within species, and whilst high amplification is a species-level trait that differs between invasive species and non-invasive species, it is intuitive that within a species enhanced ability to amplify in the invaded range would further facilitate invasion.

Observations and Recommendations: Management of Invasive Plant Species and Future Research Opportunities

The combined findings of this thesis (Chapters 2 – 5) strongly indicate that high, stage-structured fecundity is the most significant contributor to the relationship between demographic amplification and invasiveness, and that phylogenetic signal in demographic amplification might be explained by seed size and seed production as regulated by the structure of reproductive organs, which are shaped by evolutionary history among plants (Chapter 4). This finding is intuitive because a plethora of traits have been previously correlated with invasiveness but individually these may explain little variance in invasiveness. Yet demographic performance encompasses the influence of multiple traits of which fertility is the outcome.

Currently we are unable to predict from a trait to stage-specific demographic rate to demographic metric because fecundity, seed diapause and germination data remain unavailable for many species. Improved links between trait and demographic databases might permit such predictive power. We do however, propose that high fecundity be used as a predictor of plant invasiveness, and that species and genera with amplificatory life histories, should not be exported. To implement effective screening within existing invasive risk assessment protocols for the purpose of 1) preventing harmful species introductions; and 2) appropriate targeting of existing naturalised populations for eradication and control in accordance with target 9 of the IUCN 2020 Strategic Plan for Biodiversity https://www.iucn.org/theme/species/our-work/influencing-policy/convention-biological-diversity-cbd/aichi-targets, strategic collection of demographic data representative of diverse genera and reproductive strategies is required. Furthermore, our findings indicate that demographic or life history differences are most likely to be revealed using analysis of transient indices which do not assume a SSS. Such analyses should be used to investigate the relationship between demographic properties and invasiveness. We recommend greater exploration of the relationship between seed size, seed production, germination, seedling establishment and invasiveness. In relation to Chapters 2 and 3, we recommend that future work test if our results are true on a global scale, for a larger number of phylogenetically paired species that represent the full spectrum of life forms.

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