Contributed Paper

Trait differences between naturalized and invasive plant species independent of residence time and phylogeny

R. V. Gallagher,* R. P. Randall,† and M. R. Leishman*

*Department of Biological Sciences, Macquarie University, NSW 2109, Australia, email rachael.gallagher@mq.edu.au
†Invasive Species Science, Department of Agriculture and Food, WA 6151, Australia

Abstract: *The ability to predict which alien plants will transition from naturalized to invasive prior to their introduction to novel regions is a key goal for conservation and has the potential to increase the efficacy of weed risk assessment (WRA). However, multiple factors contribute to plant invasion success (e.g., functional traits, range characteristics, residence time, phylogeny), and they all must be taken into account simultaneously in order to identify meaningful correlates of invasion success. We compiled 146 pairs of phylogenetically paired (congeneric) naturalized and invasive plant species in Australia with similar minimum residence times (i.e., time since introduction in years). These pairs were used to test for differences in 5 functional traits (flowering duration, leaf size, maximum height, specific leaf area [SLA], seed mass) and 3 characteristics of species' native ranges (biome occupancy, mean annual temperature, and rainfall breadth) between naturalized and invasive species. Invasive species, on average, had larger SLA, longer flowering periods, and were taller than their congeneric naturalized relatives. Invaders also exhibited greater tolerance for different environmental conditions in the native range, where they occupied more biomes and a wider breadth of rainfall and temperature conditions than naturalized congeners. However, neither seed mass nor leaf size differed between pairs of naturalized and invasive species. A key finding was the role of SLA in distinguishing between naturalized and invasive pairs. Species with high SLA values were typically associated with faster growth rates, more rapid turnover of leaf material, and shorter lifespans than those species with low SLA. This suite of characteristics may contribute to the ability of a species to transition from naturalized to invasive across a wide range of environmental contexts and disturbance regimes. Our findings will help in the refinement of WRA protocols, and we advocate the inclusion of quantitative traits, in particular SLA, into the WRA schemes.*

Keywords: functional traits, integrative invasion science, invasion continuum, invasive species, native range characteristics, naturalized plants, residence time, sleeper weeds

Diferencia de Características entre Especies de Plantas Naturalizadas e Invasoras Independientes del Tiempo de Residencia y de la Filogenia

Resumen: *La habilidad para predecir cuáles plantas exóticas harán la transición de naturalizadas a invasoras antes de su introducción a regiones nuevas es un objetivo clave para la conservación y tiene el potencial de incrementar la eficiencia de la evaluación de riesgo de hierbas (ERH). Sin embargo, múltiples factores contribuyen al éxito invasor de las plantas (p. ej.: características funcionales, características de cobertura, tiempo de residencia, filogenia) y todos deben considerarse simultáneamente para poder identificar correlaciones significativas del éxito invasor. Recopilamos en Australia 146 parejas de especies de plantas invasoras y naturalizadas emparejadas filogenéticamente (congéneres) y con tiempos de residencia mínima similares (es decir, el tiempo transcurrido desde su introducción en años). Estas parejas se usaron para probar diferencias en cinco características funcionales (duración de la floración, tamaño de la hoja, altura máxima, área específica de la hoja [AEH], masa de la semilla) y en tres características de cobertura nativa de las especies (ocupación de bioma, temperatura media anual y amplitud de pluviosidad) entre especies invasoras*

y naturalizadas. Las especies invasoras, en promedio, tuvieron una mayor AEH, periodos de floración más largos y fueron más altas que sus parientes congéneres naturalizadas. Las invasoras también exhibieron una mayor tolerancia a diferentes condiciones ambientales en su cobertura nativa, donde ocuparon más biomas y una mayor amplitud de pluviosidad y condiciones de temperatura que sus congéneres naturalizadas. Sin embargo, ni la masa de la semilla ni el tamaño de hoja difirieron entre las parejas de especies naturalizadas e invasoras. Un hallazgo relevante fue el papel de la AEH en la distinción entre las parejas naturalizadas e invasoras. Las especies con valores altos de AEH estuvieron asociadas típicamente con tasas mayores de crecimiento, pérdida rápida de volumen de material de hojas y periodos de vida más cortos que aquellas especies con AEH baja. Este conjunto de características puede contribuir a la habilidad de las especies para llevar a cabo la transición de naturalizada a invasora a lo largo de una amplia cobertura de contextos ambientales y regímenes de perturbación. Nuestros hallazgos ayudarán en la mejora de los protocolos de ERH, y abogamos por la inclusión de las características cuantitativas, en particular la AEH, en los esquemas de ERH.

Palabras Clave: características de cobertura nativa, características funcionales, ciencia integrante de la invasión, continuo de invasión, especies invasoras, hierbas sigilosas, plantas naturalizadas, tiempo de residencia

Introduction

Why do some species become invasive when introduced to a novel environment, whereas others remain naturalized? This deceptively simple question lies at the heart of invasion science and is crucial in weed risk assessment (WRA), yet it lacks a comprehensive empirical answer. Since the 1990s progress toward understanding the invasion continuum (sensu Richardson et al. 2000) has largely been made by examining invasion correlates, such as propagule pressure (Lockwood et al. 2005), residence time (Wilson et al. 2007), phylogeny (Duncan & Williams 2002; Diez et al. 2008; Proches et al. 2008), and species' traits and biogeography (Pyšek & Richardson 2006; Leishman et al. 2007; Van Kluenen et al. 2010) in isolation, rather than together in a single analysis. As a result, robust conclusions about which species will make the shift from naturalized to invasive, and why, remain somewhat elusive (but see Milbau & Stout 2008; Dawson et al. 2009). In particular, studies that explicitly compare the traits of species which have become serious invaders with those that remain naturalized (i.e., self-sustaining populations which are yet to spread) are lacking, despite the insights that such comparisons may provide into this critical transition along the invasion continuum.

Identifying which traits effectively separate naturalized plants from invaders is an important goal for improving various forms of WRA. Preborder WRA protocols aim to prevent the introduction of potentially problematic species from foreign locations. Screening typically involves the use of a standardized set of questions on the biology and invasive behavior of the species for which permission to import is being sought, as well as an assessment of the match between the climate in the native range of the species and of the recipient region (Pheloung 2001). Current WRA protocols include some questions about the functional traits and biogeographic range of potentially invasive plants. However, WRA systems do not typically ask about key quantitative traits that have

been implicated in invasion success in previous studies (e.g., specific leaf area [SLA]) (Grotkopp & Rejmánek 2007; Leishman et al. 2007; Leishman et al. 2010) or flowering duration (Reichard & Hamilton 1997; Lake & Leishman 2004).

We used pairs of closely related species with similar residence times in Australia to identify traits and range characteristics correlated with invasion success and examined how our results could be integrated into the WRA process. The invasion continuum has 3 stages: introduction, naturalization, and invasion and spread. Around 10% of all alien plant species introduced beyond their native range will naturalize (i.e., form self-sustaining populations in the landscape) (Richardson & Pyšek 2012). From this pool of naturalized plants approximately one-tenth will go on to become serious invaders capable of rapid spread and displacement of native species.

Although a number of studies have shown the importance of residence time and phylogeny in the naturalization-invasion transition (Diez et al. 2008; Proches et al. 2008; Trueman et al. 2010), less attention has been paid to the physical, phenological, physiological, and biogeographic factors (known collectively as functional traits) that affect ecological performance and if these can be effectively used to distinguish between naturalized and invasive plants. We sought to identify which functional traits and range characteristics, if any, distinguish invasive and naturalized plants when residence time and phylogenetic relatedness are held relatively constant. Table 1 details the ecological relevance of each trait and range characteristic examined to the invasion process and the specific hypotheses tested. We focused on flowering duration, leaf size, maximum height, SLA, and seed mass because these traits have all been implicated previously in invasion success via their influential on plant strategy variation. We also examined 3 macroecological characteristics of species' ranges: breadth of mean annual temperature and precipitation (mm) encountered and number of biomes occupied. Our main aim was to identify which of these quantitative traits, if

Table 1.   The functional traits and range characteristics used to test for differences between naturalized and invasive congeneric pairs of plants with similar residence times in Australia.

Trait	Ecological relevance	Hypothesized difference in a trait of an invasive species relative a naturalized species*
Flowering duration (months)	reproductive output; increased opportunity for mutualistic plant–pollinator interactions (Crawley 1997)	longer
Leaf size (cm^2)	water balance (Parkhurst & Loucks 1972), nutrient stress strategies (Cunningham et al. 1999), light interception, and penetration to the understory (Falster & Westoby 2003)	larger
Maximum height (m)	light competition (Grime et al. 1988); correlated with metabolic rate (Enquist et al. 1998), leaf mass fraction, leaf area ratio, leaf nitrogen per area, and canopy area (Falster & Westoby 2003)	greater maximum
Seed mass (mg)	colonization, recruitment, and regeneration; traded off against seed output (Leishman et al. 2000)	smaller
SLA (cm^2/g)	carbon investment and leaf economics, resource capture, and turnover; traded off against leaf longevity (Wright et al. 2004)	higher
Biome occupancy (count)	breadth of tolerance for different abiotic conditions and ability to compete in a variety of vegetation types (Olson et al. 2001)	larger number occupied in native range
Temperature breadth in native range (°C)	ability to tolerate variation in temperature (Crawley 1997)	wider across native range
Precipitation breadth in native range (mm)	ability to tolerate variation in rainfall (Crawley 1997)	wider across their native range

For example, invasive species has a longer flowering duration.

any, correlate with invasion success and may therefore be useful for improving the predictive capacity of the WRA process.

Methods

Creating Congeneric Pairs of Naturalized and Invasive Plants

We used a comprehensive data set of the introduced flora of Australia—an updated version of Randall (2007) containing unpublished data—to create a preliminary list of all species that have been recorded as being either naturalized ($n = 3296$ species; self-sustaining populations that have not spread in the landscape) or invasive (invasive: $n = 253$ species; spreading into and outcompeting native vegetation). This list has been used in previous studies on the naturalization–invasion transition in Australian flora (Phillips et al. 2010; Diez et al. 2012; Duursma et al. 2013) and is considered an authoritative source of information on invasion stage for introduced species. The term *invasive* is only applied to serious high impact environmental or agricultural weeds (Randall 2007).

We paired congeneric naturalized and invasive species on the basis of their estimated minimum residence time

(MRT) in Australia. We estimated an MRT (length of time each species has been present) from 2 sources: the year in which the first herbarium specimen was collected and the year in which the species was first imported for sale. Herbarium records were from Australia's Virtual Herbarium (http://avh.chah.org.au/), and data on the importation of exotic species for sale in Australia were taken from commercial nursery catalogues (R. Ingram, personal communication).

Using these data, we identified 146 congeneric pairs for analyses. Wherever possible, pairings were made between species with differences in MRT of ≤10 years (61 pairs). However, to increase our sample size for comparative analyses, we allowed a difference in MRT of up to 35 years for the remaining congeneric pairs (85 pairs). We chose 35 years as a maximum difference based on the findings of a previous study (Phillips et al. 2010), which showed that although invasive species, on average, have significantly longer MRTs in Australia than naturalized species, this mean difference in MRT did not exceed 35 years. All species pairs and their residence times are provided in Supporting Information. Pairs represented a range of functional groups (16 climbers, 29 grasses, 44 herbs, and 57 trees or shrubs) with growth form consistent within congeneric pairings so that we were not

making comparisons between, for example, a tree and a grass. The data set included species from 32 families and 68 genera.

Functional Trait and Range Characteristic Data

We collated data on 5 functional traits (flowering duration, leaf size, maximum height, seed mass, SLA) and 3 native range characteristics (mean annual temperature range, mean annual precipitation range, biome occupancy) (hereafter referred to collectively as traits) (Table 1). These traits were chosen because they have been associated previously with invasion success in introduced plants (Reichard & Hamilton 1997; Lake & Leishman 2004; Van Kluenen et al. 2010; Gallagher et al. 2011; Gibson et al. 2011) but not used to specifically test for differences in naturalized and invasive species.

Data on flowering duration (112 species), maximum plant height (112 species), and leaf size (88 species) were compiled from online and published floras, taxonomic treatments, and published papers detailed in Supporting Information. Seed mass data were acquired from the Royal Botanic Gardens Kew Seed Information Database (2008 [http://data.kew.org/sid/]) (92 species). The SLA data (44 species) were collated from data sets held in our lab, and Hamilton et al. (2005) from 5 large aggregations of plant trait data: the TRY database (Kattge et al. 2011 [www.try.org]), GlopNET (Wright et al. 2004; Ordonez et al. 2010), the LEDA database (Kleyer et al. 2008). The SLA observations accessed from the TRY database were originally reported in Poschold et al. (2003), Sack and Frole (2006), and Laughlin et al. (2010). A mean value was calculated wherever multiple observations existed for a single species.

We determined the breadth of climatic conditions encountered by species in their native range by calculating the range of mean annual precipitation and temperature encountered from a long-term global climate data set following the methods outlined in Gallagher et al. (2011) and in Supporting Information.

There are some limitations to our approach and to the data sets we compiled. First, although we have taken time since introduction into Australia into account, no comprehensive data exists on introduction effort for these taxa on this continent. Although a lack of data on introduction effort does not invalidate our results, their inclusion could provide further insights into invasion success (Bucharova & Van Kleunen 2009), particularly on the impact of species that are planted widely as fodder crops throughout Australia, such as *Pennisetum ciliaris* (buffell grass). Second, although we analyzed mean trait values for species to test for correlates of invasion success, we acknowledge that functional traits do vary within species. Plasticity in traits can play a role in determining impact in specific environmental contexts, but it is not likely to have affected our results because variance around trait measurements did not significantly differ between naturalized and invasive species in a preliminary analyses (data not shown). Finally, the use of aggregated global data sets for compiling functional trait information means that data for individual species may have been collected in either the native or exotic range. Although ideally trait data would have been collected solely in the exotic Australian range, this was not feasible for a comparative study of this size, and we see no a priori reason why any differences in trait data between native and exotic ranges would affect naturalized species any more than invasive species in this study.

Statistical Analyses

We used a series of one-tailed, paired *t* tests to quantify differences in trait values between naturalized and invasive congeneric pairs with similar residence times. One-tailed tests were chosen because our hypotheses were based on a priori assumptions about the direction of trait differences, such as invaders possessing higher SLA, or being taller on average, relative to their congeneric naturalized equivalent (Table 1). All traits except flowering duration and biome occupancy were log_{10} transformed before analysis to reduce skew in the raw data. Each naturalized and invasive species was used in only one congeneric pairing for any given trait; however, some pairings were used in more than one analysis across the 8 traits examined (Supporting Information).

We also investigated the correlation structure between trait variables with Pearson correlation coefficients (*r*). This analysis was conducted to examine the independence of the trait variables with the expectation that each trait would explain an independent aspect of invasion success. Data for the 8 traits for all naturalized and invasive species were aggregated and correlation coefficients were calculated between each pairwise combination of traits. All analyses were made in SPSS (version 21; IBM Corporation, Armonk, NY, USA) and were considered significant at $\alpha = 0.05$.

It was not possible to conduct multivariate analyses on the data set due to a large number of missing values when all species–trait combinations were combined in a single matrix. That is, only 11 congeneric pairings of the 145 potential pairings had data available for all 8 traits examined. Although some traits (e.g., leaf size, SLA) may be relatively easy to collect in local populations many species occur only in relatively remote or disparate locations across Australia, which made this type of collection logistically unfeasible for us.

Results

Six of the 8 traits of naturalized and invasive species differed significantly, independent of residence time and

Table 2. Results of paired *t* tests for 5 functional traits and 3 range characteristics across congeneric pairs of naturalized and invasive plants with comparable residence times in Australia.[a]

Trait	t	df	p	Naturalized mean	Invasive mean
Flowering duration (months)	1.8	55	0.04[b]	4.68	5.54
Leaf area (cm^2)	−1.0	43	0.17	28.50	35.17
Maximum height (m)	−1.8	55	0.04[b]	4.30	5.50
Seed mass (mg)	0.5	44	0.31	39.39	41.07
SLA (cm^2/g)	−2.2	21	0.02[b]	150.07	192.11
Biome occupancy (count)	−1.9	34	0.03[b]	4.71	5.63
Temperature breadth (°C)	−1.9	34	0.04[b]	16.28	18.35
Precipitation breadth (mm)	−1.8	34	0.04[b]	2,548	3,250

[a]All trait values (except flowering duration and biome occupancy) were $\log_{10}$ transformed before analysis; however, mean values based on raw data are reported for ease of interpretation.
[b]Significant results at $\alpha = 0.05$.

Differences between naturalized and invasive congeneric pairs
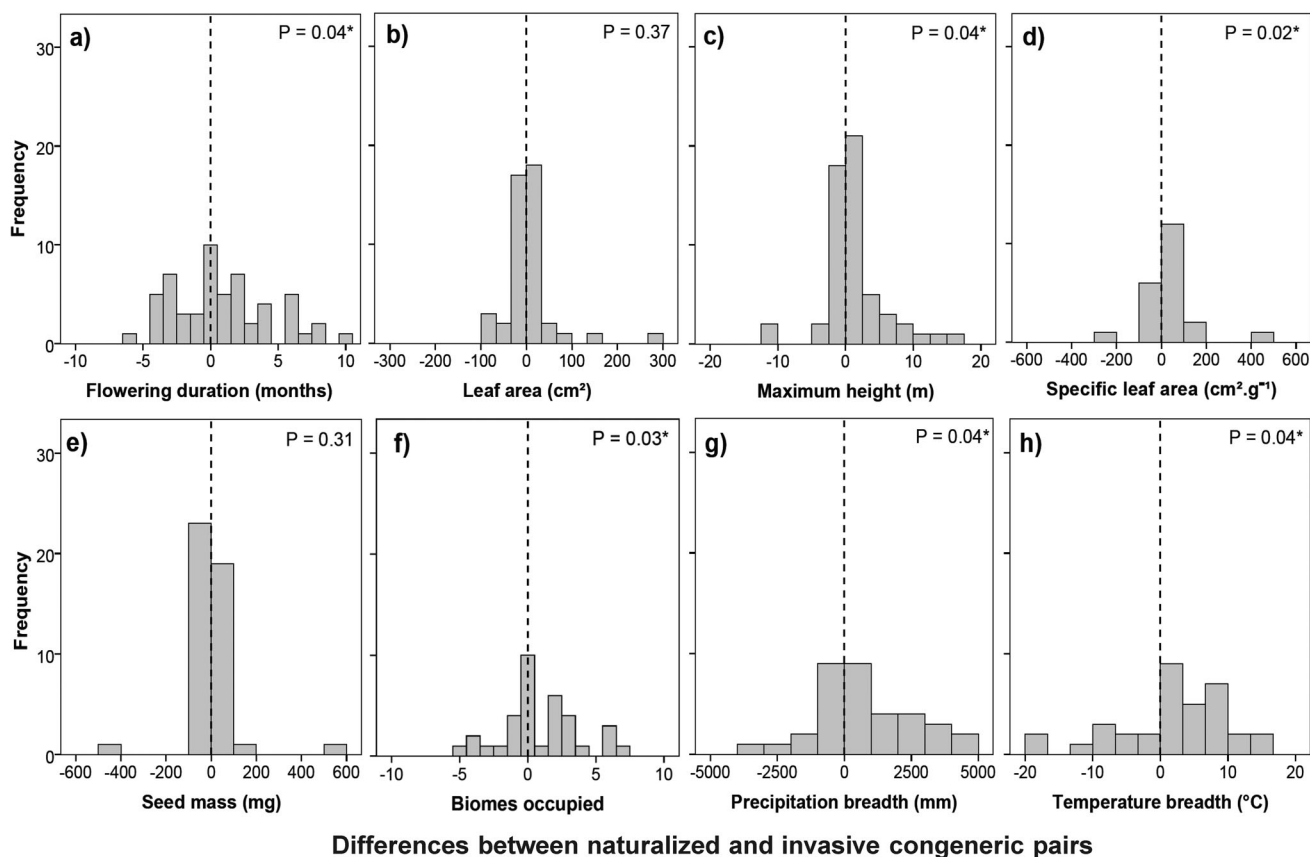
*Figure 1. Differences in 8 traits (a–h) between naturalized and invasive congeneric pairs from Australia's pool of introduced species (number of total pairs differs for each trait: [a–h] 56, 44, 56, 21, 35, 35, and 35 respectively; frequency, number of cogeneric pairs; central dashed line, no difference in traits between naturalized and invasive species; *, significant results at $\alpha = 0.05$). For example, there are 5 congeneric pairs for which the difference in SLA between naturalized and invasive congeneric pairs is −100. The number is negative for the 5 pairs because naturalized species have larger SLA than invasive species.*

phylogeny (Table 2). That is, with these 2 factors held relatively constant, paired *t* tests revealed differences ($p < 0.05$) in 3 functional traits (flowering duration, maximum height, SLA) and all 3 range characteristics (precipitation and temperature breadth,

biome occupancy) between naturalized and invasive plants (Table 2 & Fig. 1). In addition, the 5 functional traits examined were not significantly correlated (i.e., flowering duration, leaf size, maximum height, seed mass, SLA) (Table 3). Trait differences

Table 3. Pearson correlation coefficients (*r*) between 5 functional traits and 3 biogeographic range characteristics used to test for difference between congeneric pairs of naturalized and invasive plant species introduced to Australia.

Trait[a]	Flowering duration	Leaf area	Maximum height	Seed mass	SLA	Biome occupancy	Temperature breadth
Flowering duration							
Leaf area	0.11						
Maximum height	−0.13	0.05					
Seed mass	−0.06	−0.04	−0.04				
SLA	−0.12	0.17	0.17	−0.002			
Biome occupancy	0.08	0.15	0.12	−0.02	0.37[b]		
Temperature breadth	−0.02	0.10	0.09	0.05	0.2	0.57[c]	
Precipitation breadth	0.05	0.26[b]	0.09	0.08	0.22	0.37[c]	0.21

[a] *Leaf area, maximum height, seed mass, SLA, temperature breadth, and precipitation breadth were log transformed prior to analysis.*
[b] *Correlations significant at p < 0.05.*
[c] *Correlations significant at p < 0.001.*

followed hypothesized patterns: flowering duration was longer (invasive mean: 5.54 months, naturalized mean: 4.86 months), maximum height was greater (invasive mean: 5.50 m, naturalized mean: 4.3 m), and SLA larger (invasive mean: 192.11 cm^2/g, naturalized mean: 150.07 cm^2/g) on average in invasive species than in naturalized species (Table 2 & Fig. 1). Although not significant, mean leaf size was larger for invasive species relative to naturalized species as hypothesized; however, there was no trend toward smaller seed mass in invaders relative to naturalized plants (Table 2).

The breadth of mean annual temperatures and precipitation encountered in the native range and the number of biomes occupied were all greater for invasive species than for their naturalized counterparts. However, biome occupancy was significantly correlated with temperature breadth ($r = 0.57$; $p < 0.001$), precipitation breadth ($r = 0.37$; $p < 0.01$), and SLA ($r = 0.37$; $p = 0.01$). Precipitation breadth was also correlated with leaf area ($r = 0.26$; $p = 0.03$).

Discussion

Our results show that naturalized and invasive plants exhibit differences in key functional traits and range characteristics when residence time and phylogeny are held relatively constant. Six traits (SLA, height, flowering duration, rainfall breadth, temperature breadth, biome occupancy) were associated with invasion success in a large, continental pool of introduced plants in Australia. Our results highlight the value of integrating multiple factors that affect species' progression along the invasion continuum (e.g., residence time, phylogeny, traits, and biogeographic range) into a single analysis. We advocate for the inclusion of the quantitative traits associated with invasion success we identified into WRA protocols to improve their predictive accuracy.

The invasive species in this study exhibited higher values of SLA, on average, than did their congeneric naturalized relatives. Evidence suggests that SLA is highly

influential in the invasion process (Baruch & Goldstein 1999; Grotkopp et al. 2002; Leishman et al. 2007, 2010). Although multivariate studies show that traits such as growth form, flowering season, height, and native range size are associated with the probability of progressing through the invasion continuum (Gravuer et al. 2008; Hanspach et al. 2008; Milbau & Scott 2008; Bucharova & Van Kleunen 2009), no one has investigated the role of SLA. This omission likely reflects a lack of available comparative data for this trait or the time-consuming nature of its collection in the field.

A shift to higher SLA values in invasive species relative to naturalized species reflects differences in the types of strategies used to capture and deploy essential plant resources (e.g., carbon, nitrogen) between these 2 groups. High SLA values are associated with faster growth rates in invaders, particularly in the seedling stage (Grotkopp et al. 2002), and are characteristic of species at the acquisitive end of the leaf economic spectrum, which tend to deploy leaves that are rapidly turned over and relatively cheap in terms of carbon to construct (Wright et al. 2004). A capacity for rapid growth and tissue turnover may predispose species to becoming invasive by allowing them to more efficiently outcompete extant vegetation, particularly in early successional or disturbed environments. A range of studies reports higher values of SLA for invasive species relative to co-occurring native species in the field across a range of environmental conditions and disturbance regimes (Baruch & Goldstein 1999; Lake & Leishman 2004; Leishman et al. 2007, 2010). However, we found no experimental manipulations reported to date that specifically compare SLA between naturalized and invasive species, despite this being important for understanding the dynamics of the invasion continuum.

The extent to which invasive and naturalized species differ in their phenotypic plasticity under different environmental conditions is important for determining which traits correlate with invasion success in particular ecological contexts (Davidson et al. 2011). For instance, invasive species have a capacity for greater

plasticity in the expression of traits associated with light use and leaf nitrogen content relative to co-occurring natives (Funk 2008). Comparisons of this kind, particularly where limiting resources (e.g., nutrients, water) are manipulated to reconstruct different environmental conditions and naturalized and invasive species are explicitly paired, are a key area for future research into understanding the plasticity of growth traits in the naturalization–invasion transition.

Maximum height was also a correlate of invasion success in species introduced to Australia. The maximum height a species can reach in a canopy is a key indicator of light capture strategy and competitive ability (Grime et al. 1988). Plants that are able to shade out their competitors will secure more of the light available for photosynthesis; however, this strategy requires greater investment in carbon-rich support tissues, such as stems and branches. For invasive species, the ability to monopolize the light environment by shading out competing vegetation suppresses the growth and fecundity of co-occurring native species (Galbraith-Kent & Handel 2008; Hejda et al. 2009). In addition, increased plant height has been positively associated with the naturalization success of North American woody species in Europe in multivariate studies (Bucharova & Van Kleunen 2009; Urgenson et al. 2012) and with higher population spread rates of invaders (Jongejans et al. 2008). However, height has not emerged as a significant variable in other multivariate investigations of the correlates of invasion (e.g., Milbau & Stout 2008; Gallagher et al. 2011). Gallagher et al. (2011) studied trait patterning in a single clade; however, we found consistent differences in height across a number of growth forms and in species that colonize a range of landscapes. Although comparing traits among all species within a single highly invasive clade (e.g., *Acacia*: Gallagher et al. 2011; *Pinus*: Grotkopp et al. 2002) has previously provided insights into correlates of invasion success, this approach may lack generalizability across growth forms and taxonomic groups.

The invasive species in this study had flowering seasons that were, on average, almost 1 month longer than flowering seasons of the naturalized species examined. Longer flowering periods may lead to higher propagule pressure through the production of more seed over longer periods. Propagule pressure is undoubtedly a more proximal cause of invasion success than flowering duration; however, data on introduction effort and propagule pressure are particularly difficult to acquire and no comprehensive source of this type of information exists for the introduced flora of Australia. However, a longer reproductive season may increase rates of seed set by allowing greater chance of visitation by pollinators and help buffer against stochastic events, such as heat waves or frosts, which may negatively affect reproductive success (O'Neil 1999; Chrobock et al. 2013). Increases in total seed output have also been linked to longer

flowering seasons (Mason et al. 2008). The probability of seed being dispersed to new environments is likely to increase as a function of the length of the reproductive period, which may help spread invaders throughout the landscape (Pyšek & Richardson 2007). Lengthy flowering seasons have been linked to greater invasion success in species introduced to Europe (Chrobock et al. 2013) and in exotic species colonizing high nutrient sites in low-fertility sandstone vegetation in eastern Australia (Lake & Leishman 2004). There is also evidence that long flowering periods that evolved under ecological conditions in the native range may preadapt species to becoming invasive when introduced beyond their natural biogeographic limits (Jenkins & Keller 2011).

The breadth of abiotic conditions species can tolerate sets the limits of their fundamental niche (Crawley 1997). Subsequently, species with greater niche breadth for climatic factors such as temperature and precipitation are able to occupy a wider range of environments. The ecological versatility associated with wide climatic niches allows introduced species to more readily colonize and spread in novel areas outside their historical biogeographic limits (Pyšek & Richardson 2006; Gravuer et al. 2008). Our results support the idea that wide climatic niches in the native range are a common feature of successful invaders, and this idea can be used to distinguish this group of plants from naturalized species along the invasion continuum. In addition, we found that invasive species occupied a greater number of biomes, which is an integrated measure of species' tolerance to biotic and abiotic factors, in their native range than did naturalized species. Species capable of occurring a wider range of ecological settings (across multiple biomes) are more likely to go on to become invasive than other introduced plants in the continental species pool.

Biome occupancy, however, was significantly correlated with annual temperature and rainfall breadth (Table 3); therefore, these range characteristics are not fully independent measures of the ecological tolerance of species. In any practical application of our results to WRA protocols, it may be necessary to test which of rainfall, temperature, or biome breadth is the most substantial driver of differences between naturalized and invasive species in particular genera or families for which permission to import is being sought.

We found no evidence that seed mass or leaf size differed significantly between these naturalized and invasive species in Australia. One potential reason for a lack of difference in seed size between naturalized and invasive species may be our a priori decision to include only species pairs with the same growth form. Results of previous studies that show seed mass differences between invaders and other introduced or native species and do not account for growth form a priori may simply reflect the tendency for annual, herbaceous species to have both small seeds and to be overrepresented in the

invasive species pool. Annual herbs typically trade off investment in high reproductive output in a single season against individual seed size, which leads to large numbers of small seeds (Smith & Fretwell 1974). This high fecundity, coupled with a rapid life cycle, makes annual herbs one of the most common growth forms in lists of successful invaders both nationally (Reichard & Hamilton 1997) and globally (Kolar & Lodge 2001). However, results of previous studies that show small seed size as a correlate of invasiveness without accounting for growth form are likely to reflect the abundance of herbaceous annuals in exotic floras, rather than ecologically meaningful differences in seed mass. Indeed, in a global study of seed characteristics of native and invasive species, Mason et al. (2008) found no difference in seed mass between these 2 groups once growth form was taken into account.

Adding Quantitative Trait Information to WRA Schemes

Our findings may inform WRA protocols that seek to distinguish between successful and unsuccessful introductions on the basis of the physical and biogeographic characteristics of species (Hulme 2012). The 6 traits that distinguish naturalized and invasive species in our study are relatively easy and cost-effective to measure for large numbers of species; much information is already available in global databases and published floras. In particular, we encourage the addition of SLA into preborder screening procedures for plants. This trait has consistently been identified as a correlate of invasiveness in both experimental and field-based studies and would provide an informative quantitative surrogate for growth rates in comparisons among species. Quantitative estimates of growth rate would be a useful complement to qualitative questions about growth dynamics that currently feature in many WRA schemes.

New approaches will be needed if quantitative trait information is to make a useful contribution in the WRA process. For instance, it may be necessary to devise threshold values for key traits, such as SLA or height, above which species, genera, or families of plants are deemed potentially too likely to exhibit invasive behavior in certain environmental contexts. This could be achieved using data held within large-scale trait databases (e.g., TRY) (Kattge et al. 2011; LEDA: Kleyer et al. 2008) or through targeted sampling of particularly problematic groups of plants (e.g., pines or acacias).

Several other challenges to understanding the dynamics of the invasion continuum exist and to integrating these into WRA schemes, including identifying sources of data on propagule pressure and integrating these quantitative estimates into analyses. No reliable source of data on introduction effort for exotic species exists in Australia; therefore, we were unable to include this information in our analyses. Also, it will be crucial to identify how the ecological and environmental conditions under which naturalized plants have established influence the role of traits in determining a plant's ability to become invasive (i.e., the importance of environmental context) (Kueffer et al. 2013). For instance, although we show that large SLA is consistently associated with progression from naturalized to invasive independent of ecosystem conditions, the fast-growing strategy associated with large SLA may only be advantageous in early-successional, high resource, or highly disturbed environments.

Acknowledgments

Supporting Information

Information on congeneric pairs of naturalized and invasive species introduced to Australia (Appendix S1); sources of data on functional traits (Appendix S2); and methods for calculating climate niche breadth and biome occupancy (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

Baruch, Z., and G. Goldstein. 1999. Leaf construction cost, nutrient concentration, and net CO_2 assimilation of native and invasive species in Hawaii. Oecologia **121:**183–192.

Bucharova, A., and M. Van Kleunen. 2009. Introduction history and species characteristics partly explain naturalization success of North American woody species in Europe. Journal of Ecology **97:**230–238.

Chrobock, T., C. N. Weiner, M. Werner, N. Blüthgen, M. Fischer, and M. Kleunen. 2013. Effects of native pollinator specialization, self-compatibility and flowering duration of European plant species on their invasiveness elsewhere. Journal of Ecology **101:**916–923.

Crawley, M. J. 1997. Plant ecology. 2nd edition. Blackwell Publishing, Malden, MA.

Cunningham, S. A., B. Summerhayes, and M. Westoby. 1999. Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. Ecological Monographs **69:**569–588.

Davidson, A. M., M. Jennions, and A. B. Nicotra. 2011. Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. Ecology Letters **14:**419–431.

Dawson, W., D. F. Burslem, and P. E. Hulme. 2009. Factors explaining alien plant invasion success in a tropical ecosystem differ at each stage of invasion. Journal of Ecology **97:**657–665.

Diez, J. M., J. J. Sullivan, P. E. Hulme, G. Edwards, and R. P. Duncan. 2008. Darwin's naturalization conundrum: dissecting taxonomic patterns of species invasions. Ecology Letters **11:**674–681.

Diez, J. M., P. E. Hulme, and R. P. Duncan. 2012. Using prior information to build probabilistic invasive species risk assessments. Biological Invasions **14:**681–691.

Duncan, R. P., and P. A. Williams. 2002. Ecology: Darwin's naturalization hypothesis challenged. Nature **417:**608–609.

Duursma, D. E., R. V. Gallagher, E. Roger, L. Hughes, P. O. Downey, and M. R. Leishman. 2013. Next–generation invaders? Hotspots for naturalised sleeper weeds in Australia under future climates. PLos One **8**(12):e84222. DOI: 10.1371/journal.pone.0084222.

Enquist, B. J., J. H. Brown, and G. B. West. 1998. Allometric scaling of plant energetics and population density. Nature **395:**163–165.

Falster, D. S., and M. Westoby. 2003. Leaf size and angle vary widely across species: What consequences for light interception? New Phytologist **158**(3):509–525.

Funk, J. L. 2008. Differences in plasticity between invasive and native plants from a low resource environment. Journal of Ecology **96:**1162–1173.

Galbraith-Kent, S. L., and S. N. Handel. 2008. Invasive *Acer platanoides* inhibits native sapling growth in forest understorey communities. Journal of Ecology **96:**293–302.

Gallagher, R. V., M. R. Leishman, J. T. Miller, C. Hui, D. M. Richardson, J. Suda, and P. Trávníček. 2011. Invasiveness in introduced Australian acacias: the role of species traits and genome size. Diversity and Distributions **17:**884–897.

Gibson, M. R., D. M. Richardson, E. Marchante, H. Marchante, J. G. Rodger, G. N. Stone, M. Byrne, A. Fuentes-Ramírez, N. George, and C. Harris. 2011. Reproductive biology of Australian acacias: Important mediator of invasiveness? Diversity and Distributions **17:**911–933.

Gravuer, K., J. J. Sullivan, P. A. Williams, and R. P. Duncan. 2008. Strong human association with plant invasion success for *Trifolium* introductions to New Zealand. Proceedings of the National Academy of Sciences **105:**6344–6349.

Grime, J. P., J. G. Hodgson, and R. J. Hunt. 1988. Comparative plant ecology. A functional approach to common British species. Unwyn Hyman, London.

Grotkopp, E., and M. Rejmánek. 2007. High seedling relative growth rate and specific leaf area are traits of invasive species: phylogenetically independent contrasts of woody angiosperms. American Journal of Botany **94:**526–532.

Grotkopp, E., M. Rejmánek, and T. L. Rost. 2002. Toward a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 pine *Pinus*. species. The American Naturalist **159:**396–419.

Hamilton, M. A., B. R. Murray, M. W. Cadotte, G. C. Hose, A. C. Baker, C. J. Harris, and D. Licari. 2005. Life–history correlates of plant invasiveness at regional and continental scales. Ecology Letters **8**(10):1066–1074.

Hanspach, J., I. Kühn, P. Pyšek, E. Boos, and S. Klotz. 2008. Correlates of naturalization and occupancy of introduced ornamentals in Germany. Perspectives in Plant Ecology, Evolution and Systematics **10:**241–250.

Hejda, M., P. Pyšek, and V. Jarošík. 2009. Impact of invasive plants on the species richness, diversity and composition of invaded communities. Journal of Ecology **97:**393–403.

Hulme, P. E. 2012. Weed risk assessment: A way forward or a waste of time? Journal of Applied Ecology **49:**10–19.

Jenkins, C., and S. R. Keller. 2011. A phylogenetic comparative study of preadaptation for invasiveness in the genus *Silene* (Caryophyllaceae). Biological Invasions **13:**1471–1486.

Jongejans, E., K. Shea, O. Skarpaas, D. Kelly, A. W. Sheppard, and T. L. Woodburn. 2008. Dispersal and demography contributions to population spread of *Carduus nutans* in its native and invaded ranges. Journal of Ecology **96:**687–697.

Kattge, J., et al. 2011. TRY—a global database of plant traits. Global Change Biology **17:**2905–2935.

Kleyer, M., R. M. Bekker, I. C. Knevel, J. P. Bakker, K. Thompson, M. Sonnenschein, P. Poschlod, J. M. Van Groenendael, L. Klimes, et al. 2008. The LEDA Traitbase: A database of life–history traits of the Northwest European flora. Journal of Ecology **96**(6):1266–1274.

Kolar, C. S., and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. Trends in Ecology & Evolution **16:**199–204.

Kueffer, C., P. Pyšek, and D. M. Richardson. 2013. Integrative invasion science: model systems, multi-site studies, focused meta-analysis and invasion syndromes. New Phytologist **200:**615–633.

Lake, J. C., and M. R. Leishman. 2004. Invasion success of exotic plants in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. Biological Conservation **117:**215–226.

Laughlin, D. C., J. J. Leppert, M. M. Moore, and C. H. Sieg. 2010. A multi-trait test of the leaf-height-seed plant strategy scheme with 133 species from a pine forest flora. Functional Ecology **24:**493–501.

Leishman, M. R., I. J. Wright, A. T. Moles, and M. Westoby. 2000. The evolutionary ecology of seed size. In: Seeds: the ecology of regeneration in plant communities. M. Fenner, editor. CABI Publishing, Wallingford, United Kingdom.

Leishman, M. R., T. Haslehurst, A. Ares, and Z. Baruch. 2007. Leaf trait relationships of native and invasive plants: community- and global-scale comparisons. New Phytologist **176:**635–643.

Leishman, M. R., V. P. Thomson, and J. Cooke. 2010. Native and exotic invasive plants have fundamentally similar carbon capture strategies. Journal of Ecology **98:**28–42.

Lockwood, J. L., P. Cassey, and T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. Trends in Ecology & Evolution **20:**223–228.

Mason, R. A., J. Cooke, A. T. Moles, and M. R. Leishman. 2008. Reproductive output of invasive versus native plants. Global Ecology and Biogeography **17**(5):633–640.

Milbau, A., and J. C. Stout. 2008. Factors associated with alien plants transitioning from casual, to naturalized, to invasive. Conservation Biology **22:**308–317.

Olson, D. M., E. Dinerstein, E. D. Wikramanayake, N. D. Burgess, G. V. Powell, E. C. Underwood, J. A. D'amico, I. Itoua, H. E. Strand, and J. C. Morrison. 2001. Terrestrial ecoregions of the world: a new map of life on earth: a new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. BioScience **51:**933–938.

O'Neil, P. 1999. Selection on flowering time: an adaptive fitness surface for nonexistent character combinations. Ecology **80:**806–820.

Ordonez, A., I. J. Wright, and H. Olff. 2010. Functional differences between native and alien species: a global-scale comparison. Functional Ecology **24:**1353–1361.

Parkhurst, D. F., and O. L. Loucks. 1972. Optimal leaf size in relation to environment. Journal of Ecology **60:**505–537.

Pheloung, P. C. 2001. Weed risk assessment for plant introductions to Australia. Weed Risk Assessment. CSIRO Publishing, Collingwood, Victoria, Australia.

Phillips, M. L., B. R. Murray, M. R. Leishman, and R. Ingram. 2010. The naturalization to invasion transition: Are there introduction-history correlates of invasiveness in exotic plants of Australia? Austral Ecology **35:**695–703.

Poschlod, P., M. Kleyer, A. K. Jackel, A. Dannemann, and O. Tackenberg. 2003. BIOPOP—a database of plant traits and internet application for nature conservation. Folia Geobotanica **38**(3):263–271.

Proches, Ş., J. R. Wilson, D. M. Richardson, and M. Rejmánek. 2008. Searching for phylogenetic pattern in biological invasions. Global Ecology and Biogeography **17:**5–10.

Pyšek, P., and D. M. Richardson. 2006. The biogeography of naturalization in alien plants. Journal of Biogeography **33:**2040–2050.

Pyšek, P., and D. M. Richardson. 2007. Traits associated with invasiveness in alien plants: Where do we stand? Pages 97–125 in W.

Nentwig, editor. Biological invasions, ecological studies. Springer-Verlag, Berlin & Heidelberg.

Randall, R. P. 2007. The introduced flora of Australia and its weed status. CRC for Australian Weed Management, Adelaide.

Reichard, S. H., and C. W. Hamilton. 1997. Predicting invasions of woody plants introduced into North America. Conservation Biology **11:**193–203.

Richardson, D. M., and P. Pyšek. 2006. Plant invasions: merging the concepts of species invasiveness and community invisibility. Progress in Physical Geography **30:**409–431.

Richardson, D. M., and P. Pyšek. 2012. Naturalization of introduced plants: ecological drivers of biogeographical patterns. New Phytologist **196:**383–396.

Richardson, D. M., P. Pyšek, M. Rejmánek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000. Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions **6:**93–107.

Sack, L., and K. Frole. 2006. Leaf structural diversity is related to hydraulic capacity in tropical rain forest trees. Ecology **87**(2)**:** 483–491.

Smith, C. C., and S. D. Fretwell. 1974. The optimal balance between size and number of offspring. American Naturalist **108:**499–506.

Trueman, M., R. Atkinson, A. Guézou, and P. Wurm. 2010. Residence time and human-mediated propagule pressure at work in the alien flora of Galapagos. Biological Invasions **12:**3949–3960.

Urgenson, L. S., S. H. Reichard, and C. B. Halpern. 2012. Multiple competitive mechanisms underlie the effects of a strong invader on early- to late-seral tree seedlings. Journal of Ecology **100:** 1204–1215.

Van Kleunen, M., E. Weber, and M. Fischer. 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. Ecology Letters **13:**235–245.

Wilson, J. R., D. M. Richardson, M. Rouget, Ş. Procheş, M. A. Amis, L. Henderson, and W.Thuiller. 2007. Residence time and potential range: crucial considerations in modelling plant invasions. Diversity and Distributions **13:**11–22.

Wright, I. J., et al. 2004. The worldwide leaf economics spectrum. Nature **428:**821–827.