

LETTER

Life-history correlates of plant invasiveness at regional and continental scales

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Abstract

We implemented cross-species and independent-contrasts multiple regression models to compare life-history correlates of invasion success between regional and continental spatial scales among non-native plants of eastern Australia. We focussed on three life-history traits that represent major axes of variation in plant life history: specific leaf area (SLA), plant height and seed mass. After controlling for residence time and cross-correlation with other life-history traits, small seed mass was significantly and uniquely correlated with invasion success at continental and regional scales. High SLA was significantly and uniquely correlated with invasion success at the continental scale only. Plant height could not explain unique variation in invasion success at either spatial scale. Variation among spatial scales in the significance and strength of life-history relationships with invasion success suggests that the search for predictive tools of invasion need not be fruitless, as long as predictive investigations are targeted at appropriate spatial scales.

Keywords

Alien, comparative approach, introduced species, invasive, macroecology, non-native species, phylogenetic regression, seed mass, spatial scale.

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INTRODUCTION

Non-native plant species vary substantially in the degree to which they are successful in their introduced environments. Some species, such as Bridal Creeper (*Asparagus asparagoides*), proliferate rapidly in abundance and spread kilometres within a year in their introduced range (Willis *et al.* 2003). In contrast, many non-native species fail to thrive in their new environment. Understanding why some species turn out to be successful invaders while others do not is a central issue in both invasion biology and dispersal ecology.

Successful invaders often possess traits that promote invasiveness (Kolar & Lodge 2001; Cadotte *et al.* 2005a). For example, weed plant species of East Germany that can germinate their seeds over a greater proportion of the year utilize more disturbance events to become geographically widespread (Brändle *et al.* 2003). Whether successful invaders possess a distinct suite of life-history traits is not only of intrinsic interest to ecologists, it is also of fundamental importance for the prediction and management of future invaders. Time and money can be prioritized effectively if comparatively easy-to-measure life-history traits can be used

to refine assessments of the relative risks of invasiveness among a pool of non-native species.

Spatial scale of invasion is an issue of growing importance in invasion biology and dispersal ecology (Sax & Gaines 2003; Herben *et al.* 2004; Cadotte & Fukami 2005). Processes affecting patterns of biodiversity are often categorized into 'local' and 'regional' processes (Ricklefs 1987), highlighting the importance of viewing ecological mechanisms operating at different spatial scales. Local processes (competition, predation, pathogens) are determined by site characteristics and co-occurring species, while regional processes (dispersal, evolution) are characterized by dynamics occurring over larger spatial scales and longer time periods. Indeed, it has been suggested that studies at a single spatial scale are unlikely to discern the drivers of invasion patterns (Collingham *et al.* 2000; Lloret *et al.* 2004). As an illustration of the importance of considering spatial scale in biological invasions, Knight & Reich (2005) found that the amount of cover of the invading species, *Rhannus cathartica*, was negatively related to native species richness at patch scales but positively related at landscape scales. Clearly, such vastly different patterns at different spatial scales have

important ramifications for our understanding of biological invasions. In particular, the importance of spatial scale must be determined for life-history correlates of invasion success among plants, in order that predictive systems of invasions are not viewed at the wrong spatial scale. Relationships between life history and plant abundance often differ between studies (Kolar & Lodge 2001; Cadotte *et al.* 2005a). While such differences can be driven by differences in disturbance events that habitats experience (e.g. Lake & Leishman 2004), it is also possible that the spatial scales at which studies have been performed may explain inter-study variation in relationships between life-history and plant abundance (e.g. Murray *et al.* 2002a).

In the present study, we compared life-history correlates of plant invasiveness between regional and continental spatial scales. Our study focussed on a large set of non-native plant species introduced to eastern Australia since European settlement (*c.* 200 years ago). Performing our own field surveys, we determined the regional abundance of over 150 non-native plant species across 200 sites of Royal National Park, the oldest National Park in Australia. We then used the most up-to-date herbaria records from across the country to determine the continental abundance of these species. We were interested in answering the following five questions:

- (1) Do differences in life history explain variation in invasion success among non-native plant species?
- (2) Are relationships between life-history traits and plant invasion success across present-day species consistent between regional and continental spatial scales?
- (3) Are life-history correlates of plant invasiveness across present-day species the result of multiple, independent correlated evolutionary divergences between life history and invasiveness, or alternatively, one or a few major divergence events?
- (4) Does residence time (i.e. the time a non-native species has spent in the introduced range) influence the abundance of non-native plants, such that species that have had more time to spread are more abundant?
- (5) Are rates of spread different at regional and continental spatial scales?

METHODS

Conceptual approach

There are several approaches for determining the role of plant life history in successful biological invasions (Mack 1996). It is imperative that there is clarity in the question that is being asked concerning invasion success, so that the correct approach can be adopted. Conceptually, we consider it important to discuss these approaches, which include source-area, native-comparison, and target-area methods of

analysis (Pyšek *et al.* 2004), so that our reasons for adopting the target-area approach are transparent.

The source-area approach (e.g. Prinzing *et al.* 2002) answers the question, do life histories of species that become invasive from a geographic 'source' region differ from those species that do not invade from that same source region? Such an approach can characterize the traits of species that pass through the early transition phases (i.e. transport, establishment) of the invasion process to become invaders in a new region (Kolar & Lodge 2001). In this approach, it is crucial that species characteristics such as geographic origin and size of the geographic range in the native region are considered prior to consideration of the importance of life history. This is necessary in order to take into account the chance of dispersal by humans from the source area, otherwise life-history features of invading species can be confused with the circumstances associated with dispersal (Pyšek *et al.* 2004). We can not adopt this approach in the present study, because size of the geographic range and geographic origin can not be determined reliably for our study species. Invasion into Australia has taken place over the last 200 years, and many species alien to Australia had already been dispersed beyond their natural borders during this time to regions other than their native region. The size of the 'new' range of species at the time of introduction to Australia can not be quantified.

The native-comparison approach compares the life-history traits of native with non-native species in the new environment (Crawley *et al.* 1996; Cadotte & Lovett-Doust 2001; Lake & Leishman 2004). This approach answers the question, what traits of the invading species enhance their potential to increase in abundance over native species? An issue with this approach is that among a pool of species native to a study region, some native species will have become invasive because of changes in land use brought about by human activities. Thus, it is crucial that these species are accounted for in any comparisons between native and non-native species (e.g. see Leishman & Thomson 2005 for a good example of accounting for native invaders). A further difficulty of the native-comparison approach in an evolutionary framework is that the number of independent evolutionary divergences that can be compared for shifts in life history between natives and non-natives is often limited. Because one of our questions in the present study is centred on the importance of evolutionary events in biological invasions, we do not use the native-comparison approach here.

A target-area approach focuses on a pool of non-native species in a region and compares their variation in invasion success with differences in life history (Pyšek *et al.* 1995; Rejmánek & Richardson 1996; Grotkopp *et al.* 2002; Brändle *et al.* 2003; Lloret *et al.* 2004). Among a pool of non-native species that have already established in a region,

this approach answers the question, what traits distinguish successful invaders from non-native species that have not invaded successfully? An analysis employing the target-area approach should control for the influence of residence time among non-native species, prior to examination of the role of life history in invasion, to remove the potentially confounding issue that the longer a species has been in a new area, the greater the chance that it has become abundant and widespread (e.g. Pyšek *et al.* 2003). Here, we adopt the target-area approach and control for the influence of residence time.

Study location, study species and invasiveness

Royal National Park, spanning a total area of 15 068 ha, is located in eastern Australia, on the southern fringe of metropolitan Sydney. Established in 1879, it includes the first area of land to be set aside as a National Park in Australia (NPWS 2000). It is Australia's oldest, and the second oldest National Park after Yellowstone in the USA. Annual mean precipitation for the area ranges between 1143 and 1270 mm. The Park consists of a Hawkesbury Sandstone plateau up to 200 m in elevation. The plateau is characterized by steep valleys and ridges, rocky outcrops and streams punctuated by waterfalls and pools (Fairley 1995). Over 2 million people visit the Park annually, a rate of use that is exceptionally high given the Park's size. Introduced species are becoming increasingly common in the Park, with non-native plant species now comprising 20% of the local flora and an estimated 6000 ha of the Park affected by invasive plants (NPWS 2000).

We performed vegetation surveys in the Park to assess the relative invasion success of non-native species at a regional spatial scale. Vegetation surveys were carried out so as to ensure that the length and breadth of the Park were comprehensively covered. To locate a large number of field sites, we initially overlaid a clear plastic grid with grid cells of 100 m × 100 m on a 1 : 25000 topographic map of the Park. A total of 200 grid cells (sites) were selected at random using a random number generator. In the field, we randomly located a 100 m² quadrat (20 m × 5 m) along a fragment edge (adjacent to either roads, urban development, fire trails or walking tracks because of the vast majority of the undisturbed Park being free of non-native species) within each of the 200 sites. We visited each site twice, during the winter (July) and summer (December) of 2003, and identified all non-native species present (see Supplementary Material). Species were either identified *in situ* using various keys and texts (Harden 1990–1993), or specimens were collected and taken to the Royal Botanic Gardens (Sydney) for identification. Invasion success of each non-native species was estimated as regional abundance across the Park. The regional abundance of each non-native species was

determined as the proportion of the 200 sites at which it was located. We consulted National Parks and Wildlife Service (NSW) to verify that none of our sites had been cleared by vegetation regeneration activities, to ensure that estimates of regional abundance were not confounded by recent removal of weeds. To assess the continental abundance of each species and hence invasion success across the Australian continent, we used estimates of area of occupancy based on the most-up-to-date (accessed in 2004 at the Royal Botanic Gardens, Sydney) herbarium records from herbaria located across Australia (e.g. Murray *et al.* 2002b). A 100 km × 100 km grid sheet was placed over distribution maps for each species, and the number of occupied cells was tallied to estimate area of occupancy.

Residence time

Analyses of several pools of non-native species have shown that the more time non-native species have spent in their introduced ranges, the more likely they are to have become widespread (Rejmánek 2000; Pyšek *et al.* 2003; Wu *et al.* 2003; Pyšek *et al.* 2004). We tested for this temporal component of invasion in our study species. Such a test requires knowledge of the time of introduction of the study species, data that are notoriously hard to obtain (Kolar & Lodge 2001; Pyšek *et al.* 2003). From literature sources, we were able to obtain exact dates of introduction for 50 of our 152 study species (see Supplementary Material). Using records from herbarium collections across Australia, we were able to obtain dates of first collection for all of our study species (Supplementary Material). We tested whether dates of first collection could be used as surrogates of introduction times by correlating introduction date with first collection date. Our analysis revealed a highly significant positive correlation between time of introduction and first collection date [$r = 0.52$, slope = 0.36 ± 0.08 (SE), $P < 0.0001$]. Hence, minimum residence time (*sensu* Rejmánek 2000) was determined as $2005 - x$, where x represents first collection date and 2005 is the present year.

Life-history traits

Our analysis focussed on three strategically important life-history traits that represent major axes of variation in plant life history, specific leaf area (SLA), plant height, and seed mass (Westoby 1998). SLA represents light-capturing area deployed per dry mass allocated. SLA is closely correlated with other plant traits such as photosynthetic capacity, leaf N content, leaf life-span, and importantly, relative growth rate (e.g. Reich *et al.* 1997). Plant height is the simplest measure of the spectrum of strategies employed by different species for light interception, coping with heat loads, wind speeds and humidity, and represents the costs of structural

support and water transport, while seed mass represents the chance of successful dispersal by a species into an establishment opportunity and gives an indication of a seedling's ability to survive a range of hazards (Westoby 1998).

SLA measurements were made by sampling fully expanded, mature leaves from five different individuals of each species. Leaves were collected from the fullest light positions available, and leaves with herbivore or pathogen damage were not collected. Field-collected leaves were initially stored in sealed plastic bags on ice in a portable cooler, and on return to the laboratory were immediately scanned using Delta-T scan (Delta-T, Cambridge, UK). Area was measured on a one-sided basis, with petioles included if present. After scanning, leaves were placed in paper bags in an 80 °C oven for 48 h to dry leaves to constant mass, and subsequently weighed. SLA was measured as the ratio of leaf area to leaf dry mass. Plant height was measured as the maximum height a species can obtain using literature sources (e.g. Harden 1990–1993) and field observations. For estimates of seed mass, we sampled seeds from five different individuals of each species. Seeds were placed in a paper bag, and stored in a cool dry environment in the laboratory. Seeds were dried in an 80 °C oven for 48 h to achieve constant mass. Dispersal structures were then removed prior to weighing. All life-history data are provided in the Supplementary Material.

Statistical analyses

We used linear regression analysis to model bivariate relationships between residence time and regional abundance, and residence time and continental abundance. Residence time was the predictor variable in each analysis. Regional abundance, continental abundance and residence time were arcsine-square root transformed prior to analysis to approximate normality. Analysis of covariance was used to test for differences in the slopes of the two relationships. Here, spatial scale was the factor variable (regional vs. continental) and residence time was a covariate. A significant interaction term between spatial scale and residence time indicated that the slopes of the two relationships differed significantly. Standardized slopes of the regressions were used to compare increase in abundance (i.e. rate of spread) between spatial scales (Quinn & Keough 2002). Standardized values take into account the different scales of abundance, and allow valid comparison of rates of spread. The ability of regional abundance to predict continental abundance was investigated using simple linear regression analysis.

Our analyses of relationships between life-history traits (predictor variables) and regional and continental abundance were performed in three consecutive stages. Prior to

analysis, all life-history traits were ln-transformed to approximate normality. First, we built single-predictor models using simple linear regression analysis to quantify relationships between abundance at each spatial scale and each of the three life-history traits on their own. In the second stage of analysis, multiple regressions were carried out to examine the performance of each life-history trait as a predictor variable after accounting for the influence of residence time on abundance. In the third stage, residence time and all life-history traits were incorporated in multiple regression modelling to determine the importance of SLA, plant height and seed mass in explaining variation in abundance.

In multiple regressions, we were particularly interested in the unique contribution of each life-history trait (e.g. Murray *et al.* 2002b). The unique contribution of a predictor variable reflects the variation in the dependent variable that is accounted for by that predictor variable over and above the effects of the other predictors in the model. For instance, we were able to determine whether seed mass was capable of explaining significant variation in abundance independently of SLA, plant height, and residence time. Partial correlation coefficients (r_p) produced in the multiple regression models indicate the strength of the unique associations.

We performed both cross-species and independent contrasts analyses (see Murray *et al.* 2002b). Cross-species analysis did not explicitly consider phylogenetic relatedness among species. A normal error structure with an identity link was employed in all cross-species models (Crawley 1993). A second analysis that explicitly considered phylogenetic relatedness among species was performed (Harvey & Pagel 1991). This independent contrasts analysis was carried out by implementation of the phylogenetic regression (PHYLO.GLM, version 1.03; Grafen 1989). When used in conjunction with cross-species analysis, independent contrasts can reveal important evolutionary underpinnings of patterns emerging across present-day species (Cadotte *et al.* 2005a). For instance, if a significant negative cross-species correlation between seed mass and invasiveness disappears in independent contrasts analysis, this indicates that the present-day relationship is the result of one or a small number of independent, correlated evolutionary divergences between small seed mass and invasiveness. On the other hand, if the cross-species relationship persists in independent contrasts analysis, this indicates that there have been multiple, independent evolutionary divergence correlations between small seed mass and invasiveness.

Phylogenetic regression models require the construction and coding of a working phylogeny. This process was automated by the Phylomatic database, with details on full assembly rules and source information for the phylogeny

available at the Phylomatic website (Webb & Donoghue 2002). Phylomatic constructs a phylogenetic tree based on a phylogenetic 'mega-tree' assembled from global data sets. We then coded this phylogenetic tree so that each node in the tree had its own unique number, allowing each node (i.e. evolutionary divergence) to be analysed as an independent unit in the phylogenetic regression (Grafen 1989). Path segment lengths for the phylogeny were calculated in phylogenetic regressions by assigning a height to each node that was one less than the number of species below or at that node in the tree (Grafen 1989). The working phylogeny is available from the authors on request.

RESULTS

Residence time and abundance

Residence time was a significant predictor of both regional abundance ($r^2 = 0.06$, $F_{1,146} = 9.41$, $P = 0.003$) and continental abundance ($r^2 = 0.33$, $F_{1,145} = 71.68$, $P < 0.001$) across all species. The standardized slopes of the two regressions (regional abundance, $\beta = 0.25$; continental abundance, $\beta = 0.58$) were significantly different ($F_{1,291} = 4.43$, $P = 0.04$). The higher slope shown for the relationship between residence time and continental abundance indicates that the rate of spread of non-native species is significantly faster at a continental scale than at a regional scale. Regional abundance was a significant predictor of continental abundance across all species, as evidenced by the significant positive relationship between the two ($r^2 = 0.12$, $F_{1,149} = 20.42$, $P \leq 0.001$).

Cross-species patterns: life-history, abundance and spatial scale

All three life-history traits were significantly related to regional and continental abundance in simple linear regressions (Table 1). SLA was positively correlated with regional and continental abundance, while plant height and seed mass were negatively correlated with regional and continental abundance.

Once residence time and the influence of the other life-history traits were controlled in multiple regression analysis, SLA was no longer significantly related to regional abundance (Table 1). A significant negative relationship persisted between plant height and regional abundance when residence time was the only other control variable, however, the significance of this relationship disappeared after adding SLA and seed mass as control variables (Table 1). Only seed mass was significantly and uniquely related to regional abundance in multiple regression analysis (Table 1). At a continental scale, SLA was positively and seed mass negatively related significantly and uniquely to abundance, both in multiple regressions that controlled only for residence time and in regressions that controlled for residence time and the other life-history traits (Table 1). A significant negative relationship persisted between plant height and continental abundance when residence time was the only other control variable. However, this significant relationship disappeared after all other variables were entered into a multiple regression examining the unique contribution of plant height to continental abundance (Table 1).

Trait	Single		Control (rt)		Multiple	
	$r_{(d.f.)}$	<i>P</i> -value	r_p (d.f.)	<i>P</i> -value	r_p (d.f.)	<i>P</i> -value
(a) Regional						
SLA	0.17 _(1,138)	0.04	0.14 _(2,133)	0.11	0.07 _(4,108)	0.49
Height	-0.21 _(1,150)	0.009	-0.21 _(2,145)	0.01	-0.07 _(4,108)	0.46
Seed mass	-0.27 _(1,118)	0.003	-0.26 _(2,116)	0.004	-0.19 _(4,108)	0.04
(b) Continental						
SLA	0.30 _(1,137)	< 0.001	0.23 _(2,132)	0.007	0.21 _(4,108)	0.03
Height	-0.17 _(1,149)	0.03	-0.21 _(2,144)	0.01	0.00 _(4,108)	0.97
Seed mass	-0.29 _(1,118)	0.001	-0.32 _(2,116)	< 0.001	-0.23 _(4,108)	0.02

Table 1 Cross-species regressions between life-history traits and (a) regional and (b) continental abundance

Simple regressions ('single' column) were performed between each trait and abundance at each spatial scale (r is the correlation coefficient, d.f. the degrees of freedom). In the 'control' analysis, the independent effects of each trait were examined after controlling for residence time, while in the 'multiple' analysis, the independent effects of each trait were examined after controlling for the effects of residence time and the other life-history traits (r_p is the partial correlation coefficient in these analyses).

Significant relationships are in bold.

Table 2 Phylogenetic regressions between life-history traits and (a) regional and (b) continental abundance

Trait	Single		Control (rt)		Multiple	
	$r_{(d.f.)}$	<i>P</i> -value	r_p (d.f.)	<i>P</i> -value	r_p (d.f.)	<i>P</i> -value
(a) Regional						
SLA	0.24 _(1,67)	0.04	0.19 _(1,69)	0.12	0.08 _(1,57)	0.56
Height	-0.30 _(1,71)	0.01	-0.27 _(1,73)	0.02	-0.11 _(1,57)	0.43
Seed mass	-0.35 _(1,62)	0.005	-0.35 _(1,61)	0.005	-0.27 _(1,57)	0.04
(b) Continental						
SLA	0.42 _(1,70)	< 0.001	0.33 _(1,69)	0.005	0.29 _(1,57)	0.02
Height	-0.23 _(1,74)	0.04	-0.26 _(1,73)	0.02	0.01 _(1,57)	0.96
Seed mass	-0.39 _(1,62)	0.002	-0.41 _(1,60)	0.001	-0.31 _(1,57)	0.02

Simple regressions ('single' column) were performed between each trait and abundance at each spatial scale (r is the correlation coefficient, d.f. the degrees of freedom). In the 'control' analysis, the independent effects of each trait were examined after controlling for residence time, while in the 'multiple' analysis, the independent effects of each trait were examined after controlling for the effects of residence time and the other life-history traits (r_p is the partial correlation coefficient in these analyses).

Significant relationships are in bold.

Evolutionary patterns underpinning cross-species patterns

Phylogenetic regression analyses of evolutionary divergence correlations between life-history traits and invasion success produced qualitatively similar findings to cross-species regressions (Table 2). Importantly, after controlling for residence time and the effects of the other life-history traits, SLA was positively and seed mass was negatively correlated with invasion success throughout the phylogeny of the study species. This indicates that patterns emerging across present-day species are the product of multiple, independent evolutionary divergences.

DISCUSSION

This study set out to examine how evolutionary history, life-history traits and ecological scale all interact to drive patterns of species invasions. Inderjit *et al.* (2005) highlighted 15 hypotheses purporting to explain patterns of plant invasions. These hypotheses address ecological interactions, evolutionary history and life-history traits singularly, but our results give credence to the idea that these processes may not be mutually exclusive, and that a spatially explicit or comparative approach can shed some light on how these processes interact. An invasion is not a process occurring at a single spatial scale, but is a convergence of explanations from biogeographical, regional and local scales (Cadotte *et al.* 2005b).

In relation to our first question, we found that inter-specific differences in life history were related to invasion success. However, in answer to our second question, we found that relationships between life-history traits and plant invasion success were not entirely consistent between

regional and continental spatial scales. Small seed mass was correlated with high abundance at both continental and regional scales, with predictive power decreasing slightly with a decrease in spatial scale, and high SLA was correlated with high abundance at the continental scale only.

Small seed mass is correlated tightly with increased seed output (relative to the production of large seeds from a fixed finite resource, e.g. Henery & Westoby 2001). In addition, small seeds of non-Australian origin generally persist longer in the soil than large seeds (Thompson *et al.* 1993). Small seed mass is usually indicative of a wind dispersal syndrome (Howe & Smallwood 1982). The abundant production of small, long-lived seeds that are well dispersed is a characteristic of plants that are adapted for rapid colonization of disturbed habitats (Groves 1992). Non-native species with such traits are likely to be successful invaders in new regions where habitats have been disturbed by human activities (Rejmánek & Richardson 1996; Cadotte & Lovett-Doust 2001; Grotkopp *et al.* 2002; Lloret *et al.* 2004).

In Australia, vast areas of land at the regional and continental scale have been cleared and disturbed by humans. Our findings show that small seed mass is a key trait in invasion success at multiple spatial scales where disturbance has been widespread. Interestingly, we found that the relationship between seed mass and invasion success was slightly weaker at regional spatial scales than across the continent (Table 1 and 2), indicating a decrease in predictive power of seed mass for invasion success with decreasing spatial scale. In fact, at local scales in eastern Australia, small seed mass does not correlate significantly with invasion success at all (Lake & Leishman 2004). Colonization opportunities must become spatially more

limiting at local and regional vs. continental spatial scales, and thus seed mass becomes a more important predictor of invasion success at large vs. small spatial scales.

Species with high SLA were more successful invaders than low-SLA species at the continental scale. Like small seed mass, high SLA is a trait expected of rapidly colonizing plant species (Grotkopp *et al.* 2002). High SLA is well correlated with short leaf lifespan and fast growth rate (Wright & Westoby 1999). The ability to produce leaves with an increased surface area (relative to the mass invested in leaf construction) rapidly, and to avoid significant investment of biomass in long-lasting structures, is critical in disturbed habitats where fast growth is paramount. High SLA has also been shown to be important among successful invaders within local communities in eastern Australia (Lake & Leishman 2004). Why then do we find that SLA drops out as a significant predictor of invasion success at the regional scale? We suggest that SLA becomes less important because of limitations to establishment opportunities (as opposed to colonization opportunities in the case of seed mass). However, that SLA drops out as a significant predictor of invasion success at the regional scale warrants further investigation. We suggest that the reappearance of SLA as a predictor within local communities might simply be because the analysis of Lake & Leishman (2004) did not account for cross-correlation with other life-history traits. In other words, SLA might be a secondary correlate of invasion success within communities. This is supported by the fact that we found SLA to be important at the regional scale when considered on its own in models, without accounting for the influence of other life-history traits (Table 1 and 2).

Our comparative analyses were performed within an evolutionary framework. Our third question asked whether life-history correlates of plant invasiveness across present-day species are the result of multiple, independent correlated evolutionary divergences between life history and invasiveness, or alternatively, one or a few major divergence events. Qualitatively, the cross-species and independent contrasts models concurred with the same relationships emerging between life history and invasion success in both sets of analyses. This indicates that throughout the phylogeny of the non-native species examined here, there have been multiple and independent correlated evolutionary divergences between invasion success and (i) small seed mass at regional and continental scales; and (ii) SLA at the continental spatial scale. The consistency of relationships between the cross-species and independent contrasts models, and the consistent correlative evidence for small seed mass and high SLA to be related to invasion success suggests that these traits might be efficient attributes for use in screening imported species for their invasive potential (Fisher & Owens 2004).

Our fourth and fifth questions asked whether residence time influences the abundance of non-native plants, and whether rates of spread differ between regional and continental spatial scales. In accordance with other published studies (Rejmánek 2000; Pyšek *et al.* 2003; Wu *et al.* 2003; Pyšek *et al.* 2004), we found that the longer a non-native species has been in the introduced range, the more abundant it is likely to be. An important difference in the influence of residence time emerged between the two spatial scales. The slope of the relationship between residence time and abundance was significantly greater at the continental scale compared with the regional scale. It may seem counterintuitive to state that invaders spread faster at a continental scale. Collingham *et al.* (2000) also found that invasions spread fast at coarser vs. finer scales. Several explanations may shed light on this pattern. Regional-scale environmental heterogeneity may limit the number of sites species can invade regionally, while being of little consequence at larger spatial scales. For example, altitudinal gradients may limit where a species can persist within any one region (e.g. Whittaker 1956), but specific altitudes may be widespread throughout an ecoregion (Rahbek 2005).

Even if the environment were relatively homogeneous at the regional scale, communities would likely still vary because of biotic processes (Drake 1991; Cadotte & Fukami 2005). At smaller scales, communities are thought to exhibit 'biotic resistance' to species invasions (e.g. Elton 1958; Shea & Chesson 2002). Newly arriving species will face a suite of enemies, which represent negative interactions limiting the new species success (e.g. Agrawal & Kotanen 2003). This means that some community assemblages will be more invasion-prone than others. Like environmental heterogeneity, community assemblage variation may be limiting regionally, but pervasive enough continentally.

CONCLUSION

An ongoing debate in invasion biology is whether invasions are predictable, with proponents arguing in the affirmative (e.g. Kolar & Lodge 2001) and the negative (e.g. Williamson 1999). We believe that context-explicit approaches (e.g. Lake & Leishman 2004) can resolve this apparent conundrum. Here, we demonstrate that spatial scale is clearly an important factor that must be considered in predictive systems of invasion success. We show that the type of relationships useful for prediction (i.e. residence time and abundance, and life-history correlates) are weakened as the scale of observations moves from the continent to the region. Whereas patterns at extremely large spatial scales may be robust against the vagaries of environmental and biotic heterogeneity, the regional scale is sensitive to them.

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REFERENCES

- Agrawal, A.A. & Kotanen, P.M. (2003). Herbivores and the success of exotic plants: a phylogenetically controlled experiment. *Ecol. Lett.*, 6, 712–715.
- Brändle, M., Stadler, J., Klotz, S. & Brandl, R. (2003). Distributional range size of weedy plant species is correlated to germination patterns. *Ecology*, 84, 136–144.
- Cadotte, M.W. & Fukami, T. (2005). Dispersal, spatial scale, and species diversity in a hierarchically structured experimental landscape. *Ecol. Lett.*, 8, 548–557.
- Cadotte, M.W. & Lovett-Doust, J. (2001). Ecological and taxonomic differences between native and introduced plants of southwestern Ontario. *Ecoscience*, 8, 230–238.
- Cadotte, M.W., Murray, B.R. & Lovett-Doust, J. (2005a). Ecological patterns and biological invasions: using regional species inventories in macroecology. *Biol. Inv.* (in press).
- Cadotte, M.W., McMahon, S.M. & Fukami, T. (2005b). Spatially dependent processes in invasions. In: *Conceptual Ecology and Invasions Biology: Reciprocal Approaches to Nature* (eds Cadotte, M.W., McMahon, S.M. & Fukami, T.). Springer, New York (in press).
- Collingham, Y.C., Wadsworth, R.A., Willis, S.G., Huntley, B. & Hulme, P.E. (2000). Predicting the spatial distribution of alien riparian species: issue of spatial scale and extent. *J. Appl. Ecol.*, 37 (Suppl. 1), 13–27.
- Crawley, M.J. (1993). *GLIM for Ecologists*. Blackwell Scientific, Oxford.
- Crawley, M.J., Harvey, P.H. & Purvis, A. (1996). Comparative ecology of the native and alien floras of the British Isles. *Phil. Trans. R. Soc. Lond. B*, 351, 1251–1259.
- Drake, J.A. (1991). Community-assembly mechanics and the structure of an experimental species ensemble. *Am. Nat.*, 137, 1–26.
- Elton, C.S. (1958). *The Ecology of Invasions by Plants and Animals*. Methuen, London.
- Fairley, A. (1995). *Discovering Royal National Park on Foot*. Envirobook, Sydney.
- Fisher, D.O. & Owens, I.P.F. (2004). The comparative method in conservation biology. *Trends Ecol. Evol.*, 19, 391–398.
- Grafen, A. (1989). The phylogenetic regression. *Phil. Trans. R. Soc. Lond. B*, 326, 119–157.
- Grotkopp, E., Rejmánek, M. & Rost, T.L. (2002). Toward a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 Pine (*Pinus*) species. *Am. Nat.*, 159, 396–419.
- Groves, R.H. (1992). *Weed Ecology, Biology and Spread*. Proceedings of the First International Weed Control Congress, Melbourne, Australia, pp. 83–88.
- Harden, G.J. (1990–1993). *Flora of New South Wales*. New South Wales University Press, Sydney.
- Harvey, P.H. & Pagel, M.D. (1991). *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford.
- Henery, M. & Westoby, M. (2001). Seed mass and seed nutrient content as predictors of seed output variation between species. *Oikos*, 92, 479–490.
- Herben, T., Mandák, B., Bimova, K. & Munzbergova, Z. (2004). Invasibility and species richness of a community: a neutral model and a survey of published data. *Ecology*, 85, 3223–3233.
- Howe, H.F. & Smallwood, J. (1982). Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.*, 13, 201–228.
- Inderjit, Cadotte, M.W. & Colautti, R.I. (2005). The ecology of biological invasions: past, present and future. In: *Invasive Plants: Ecological and Agricultural Aspects* (ed. Inderjit). Birkhauser, Boston, pp. 19–43.
- Knight, K.S. & Reich, P.B. (2005). Opposite relationships between invisibility and native species richness at patch versus landscape scales. *Oikos*, 109, 81–88.
- Kolar, C.S. & Lodge, D.M. (2001). Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.*, 16, 199–204.
- Lake, J.C. & Leishman, M.R. (2004). Invasion success of exotic plants in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. *Biol. Conserv.*, 117, 215–226.
- Leishman, M.R. & Thomson, V.P. (2005). Experimental evidence for the effects of additional water, nutrients and physical disturbance on invasive plants in low fertility Hawkesbury Sandstone soils, Sydney, Australia. *J. Ecol.*, 93, 38–49.
- Lloret, F., Médail, F., Brundu, G. & Hulme, P. (2004). Local and regional abundance of exotic plant species on Mediterranean islands: are species traits important? *Global Ecol. Biogeogr.*, 13, 37–45.
- Mack, R.N. (1996). Predicting the identity and fate of plant invaders: emergent and emerging approaches. *Biol. Conserv.*, 78, 107–121.
- Murray, B.R., Thrall, P.H., Gill, A.M. & Nicotra, A.B. (2002a). How plant life-history and ecological traits relate to species rarity and commonness at varying spatial scales. *Aust. Ecol.*, 27, 291–310.
- Murray, B.R., Thrall, P.H. & Lepschi, B.J. (2002b). Relating species rarity to life history in plants of eastern Australia. *Evol. Ecol. Res.*, 4, 937–950.
- NPWS (2000). *Royal National Park, Heathcote National Park and Garawarra State Recreation Area: Plan of Management*. NSW National Parks and Wildlife Service, Hurstville.
- Prinzing, A., Durka, W., Klotz, S. & Brandl, R. (2002). Which species become aliens? *Evol. Ecol. Res.*, 4, 385–405.
- Pyšek, P., Prach, K. & Šmilauer, P. (1995). Relating invasion success to plant traits: an analysis of the Czech alien flora. In: *Plant Invasions – General Aspects and Special Problems* (eds Pyšek, P., Prach, K., Rejmánek, M. & Wade, M.). SPB Academic Publishing, Amsterdam, pp. 39–60.
- Pyšek, P., Sádlo, J., Mandák, B. & Jarošík, V. (2003). Czech alien flora and the historical pattern of its formation: what came first to Central Europe? *Oecologia*, 135, 122–130.
- Pyšek, P., Richardson, D.M. & Williamson, M. (2004). Predicting and explaining plant invasions through analysis of source area floras: some critical considerations. *Divers. Distrib.*, 10, 179–187.

- Quinn, G.P. & Keough, M.J. (2002). *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge.
- Rahbek, C. (2005). The role of spatial scale and the perception of large-scale species-richness patterns. *Ecol. Lett.*, 8, 224–239.
- Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997). From tropics to tundra: global convergence in plant functioning. *P. Natl. Acad. Sci. USA*, 94, 13730–13734.
- Rejmánek, M. (2000). Invasive plants: approaches and predictions. *Aust. Ecol.*, 25, 497–506.
- Rejmánek, M. & Richardson, D.M. (1996). What attributes make some plant species more invasive? *Ecology*, 77, 1655–1661.
- Ricklefs, R.E. (1987). Community diversity: relative roles of local and regional processes. *Science*, 235, 167–171.
- Sax, D.F. & Gaines, S.D. (2003). Species diversity: from global decreases to local increases. *Trends Ecol. Evol.*, 18, 561–566.
- Shea, K. & Chesson, P. (2002). Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.*, 17, 170–176.
- Thompson, K., Band, S.R. & Hodgson, J.G. (1993). Seed size and shape predict persistence in soil. *Funct. Ecol.*, 7, 236–241.
- Webb, C.O. & Donoghue, M.J. (2002). Phylomatic: a database for applied phylogenetics. Available at: <<http://www.phylodiversity.net/phylomatic>>.
- Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil*, 199, 213–227.
- Whittaker, R.H. (1956). Vegetation of the Great Smoky Mountains. *Ecol. Monogr.*, 26, 1–80.
- Williamson, M.H. (1999). Invasions. *Ecography*, 22, 5–12.
- Willis, A.J., McKay, R., Vranjic, J.A., Kilby, M.J. & Groves, R.H. (2003). Comparative seed ecology of the endangered shrub, *Pimelea spicata* and a threatening weed, Bridal Creeper: smoke, heat and other fire-related germination cues. *Ecol. Manage. Rest.*, 4, 55–65.
- Wright, I.J. & Westoby, M. (1999). Differences in seedling growth behaviour among species: trait correlations across species, and trait shifts along nutrient compared to rainfall gradients. *J. Ecol.*, 87, 85–97.
- Wu, S.H., Chaw, S. & Rejmánek, M. (2003). Naturalized Fabaceae (Leguminosae) species in Taiwan: the first approximation. *Bot. Bull. Acad. Sinica*, 44, 59–66.

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article from <http://www.Blackwell-Synergy.com>:

Appendix S1 A list of non-native species of eastern Australia assessed for regional and continental abundance.

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