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Investment in seed dispersal structures is linked to invasiveness in exotic plant species of south-eastern Australia

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Abstract Naturalized plant species disperse their populations over considerable distances to become invasive. We tested the hypothesis that this shift from naturalization to invasion is facilitated by increased investment of resources in seed dispersal appendages, using an assemblage of naturalized plants of south-eastern Australia. Compared with non-invasive species, we found in both cross-species and independent-contrasts analyses that invasive species invested more heavily in seed dispersal appendages, regardless of the structure present on the seed associated with the mode of dispersal (e.g., wings versus fleshy fruits). Invasive species such as *Lonicera japonica*, *Hedera Helix* and *Acetosa sagittata* were found to invest as much as 60–70% of total diaspore mass in dispersal appendages. The positive relationship between dispersal investment and invasion success was still prevalent after controlling for the effects of plant growth form, seed mass and capacity for vegetative growth. Our findings demonstrate that a plant's investment in dispersal appendages helps to overcome the dispersal barrier in the shift from naturalization to invasion.

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Introduction

The invasive spread of exotic plant species into new geographic regions is widely recognised as a major threat to global biodiversity (Millennium Ecosystem Assessment 2005). Invasive plant species disrupt native plant and animal assemblages, often bringing about significant reductions in native species richness (Robson et al. 2009) and considerable alterations to ecosystem functioning (Miller and Gorchov 2004). Understanding how exotic species become invasive is central to efforts directed towards improving management efficiency and prioritizing the eradication of detrimental invasive species (Richardson et al. 2000; Bradshaw et al. 2008; Pyšek et al. 2008). In this context, the identification of attributes of exotic plant species that are linked to invasiveness is an important step in understanding the dynamics of biological invasions (Baker 1965; Rejmánek and Richardson 1996; Alpert et al. 2000; Kolar and Lodge 2001; Cadotte et al. 2006; Richardson and Pyšek 2006; Pyšek and Richardson 2007; Phillips et al. 2010).

Although many exotic plant species become naturalized following their introduction into new regions, only a subset of naturalized species become

invasive (e.g., Groves et al. 2005). To be a successful invader, an exotic plant species that disperses by seed needs to disperse its populations over considerable distances from sites of introduction (more than 100 m over less than 50 years, Richardson et al. 2000) in order to shift from the state of being naturalised to the state of being invasive. This suggests that naturalized invasive species that spread by seed possess enhanced strategies for seed dispersal that are either absent or at least not as prevalent in naturalized species that are not invasive. At present, few studies have explicitly examined seed dispersal strategies in relation to the transitioning of exotic species between the states of naturalization and invasion (reviewed in Kolar and Lodge 2001; Pyšek and Richardson 2007), despite the inherent importance of dispersal in defining the transition between these states (Richardson et al. 2000).

Methods of seed dispersal vary substantially among plant species (Hughes et al. 1994). However, the evidence for particular modes of seed dispersal being linked to invasion success is equivocal, with some studies reporting significant relationships between particular dispersal modes and invasiveness and others finding no significant patterns (Cadotte et al. 2006). Here, we adopt a different strategy to examine how dispersal strategies might be linked to invasion success. Given the wide range of interspecific variation in the amount of resources that species invest in dispersal appendages associated with their seeds (e.g., Edwards and Westoby 1996), we asked whether species that invest comparatively more in seed dispersal structures are more likely to be successful invaders. We tested the hypothesis that larger investment in dispersal appendages leads to an increased chance of species dispersing their populations over considerable distances from sites of introduction and thus to a shift from a naturalized state to an invasive one. Dispersal appendages in this context refer to the mass investment in structural features of the seed that facilitate dispersal, relative to the seed (embryo plus endosperm) within the diaspore. Our study focussed on naturalized plant species of the oldest nature reserve in Australia, Royal National Park (south-eastern Australia, New South Wales), a region of Australia that has been exposed to the incursion of exotic plants since European settlement nearly 220 years ago (Hamilton et al. 2005).

Methods

Study area

We employed a target-area approach (sensu Pyšek et al. 2004) to compare traits related to invasion success among a pool of exotic plant species resident within a geographic region (Pyšek et al. 1995; Grotkopp et al. 2002; Hamilton et al. 2005). Our study focussed on the naturalized exotic plant flora of Royal National Park (latitude 34° 02′ 24″ to 34° 14′ 24″ S; longitude 151° 10′ 12″ to 150° 55′ 48″ E), a region of south-eastern Australia which spans a total area of 15 068 ha and which is located 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 1,143 and 1,270 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. Naturalized species are becoming increasingly common in the Park, with exotic plant species now comprising 20% of the local flora and an estimated 6,000 ha of the Park affected by invasive plants (NPWS 2000).

Study species

The dataset for this study was comprised of 88 species from a total of 28 taxonomic families, all of which are naturalized in Australia (Table 1). A total of 42 species in the dataset are invasive across Australia while the remaining 46 species are considered non-invasive. Our list of study species was compiled by first consulting a recent inventory of the introduced flora of Royal National Park (Hamilton et al. 2005). From this source of 150 exotic species, we extracted all species known to be naturalized in Australia using information from the latest compendium of the introduced flora of Australia (Randall 2007). This compendium not only comprehensively lists all naturalized plant species in Australia (category 'N' species), it also identifies which species are

Table 1 The dataset of naturalized exotic plant species of Royal National Park (south-eastern Australia) and attribute values for invasion status (0 = non-invasive, 1 = invasive), minimum residence time (MRT = 2009—year of first record, where 2009 is the present year), growth form (grass, herb, shrub, tree, climber), seed mass (total diaspore mass, mg, without mass of dispersal structures) and capacity for vegetative spread (1 = no observed capacity, 2 = observed capacity for vegetative spread)

Species	Family	MRT	Status	Growth form	Seed mass (mg)	Vegetative growth
Acetosa sagittata	Polygonaceae	110	1	Climber	1.09	2
Ageratina adenophora	Asteraceae	137	1	Herb	0.04	2
Ageratina riparia	Asteraceae	134	1	Herb	0.07	2
Anagallis arvensis	Myrsinaceae	205	1	Herb	0.33	1
Andropogon virginicus	Poaceae	74	1	Grass	0.16	1
Araujia sericifera	Apocynaceae	133	1	Climber	7.03	1
Asparagus aethiopicus	Asparagaceae	119	1	Shrub	50.32	2
Asparagus asparagoides	Asparagaceae	152	1	Climber	8.19	2
Axonopus fissifolius	Poaceae	112	0	Grass	0.31	2
Bidens pilosa	Asteraceae	239	1	Herb	1.30	1
Briza maxima	Poaceae	181	1	Grass	1.66	1
Briza minor	Poaceae	205	0	Grass	0.14	1
Bromus catharticus	Poaceae	125	0	Grass	7.56	1
Capsella bursa-pastoris	Brassicaceae	124	0	Herb	0.05	1
Cardamine hirsuta	Brassicaceae	61	1	Herb	0.06	1
Centaurium erythraea	Gentianaceae	123	0	Herb	0.01	1
Cerastium glomeratum	Caryophyllaceae	205	0	Herb	0.04	1
Cestrum parqui	Solanaceae	111	1	Shrub	4.32	2
Chrysanthemoides monilifera	Asteraceae	157	1	Shrub	28.64	2
Cinnamomum camphora	Lauraceae	182	1	Tree	106.20	1
Conyza sumatrensis	Asteraceae	166	0	Herb	0.03	1
Coreopsis lanceolata	Asteraceae	171	1	Herb	1.12	2
Cyclospermum leptophyllum	Apiaceae	126	0	Herb	0.23	1
Cyperus eragrostis	Cyperaceae	149	0	Herb	0.16	2
Duchesnea indica	Rosaceae	123	0	Herb	0.34	2
Ehrharta erecta	Poaceae	78	1	Grass	0.99	2
Eleusine indica	Poaceae	118	0	Grass	0.54	2
Eragrostis curvula	Poaceae	109	1	Grass	0.14	2
Eragrostis tenuifolia	Poaceae	75	0	Grass	0.12	1
Facelis retusa	Asteraceae	70	0	Herb	0.15	1
Foeniculum vulgare	Apiaceae	206	0	Herb	1.07	2
Galinsoga parviflora	Asteraceae	143	1	Herb	0.17	1
Gamochaeta americana	Asteraceae	109	0	Herb	0.01	1
Gamochaeta calviceps	Asteraceae	107	0	Herb	0.01	1
Gomphocarpus fruticosus	Apocynaceae	207	0	Shrub	7.00	2
Hedera helix	Araliaceae	181	1	Climber	10.78	2
Hydrocotyle bonariensis	Apiaceae	116	1	Herb	0.52	2
Hypochaeris glabra	Asteraceae	164	0	Herb	0.42	1
Hypochaeris radicata	Asteraceae	143	0	Herb	0.88	1
Jacaranda mimosifolia	Bignoniaceae	127	0	Tree	18.53	1

Table 1 continued

Species	Family	MRT	Status	Growth form	Seed mass (mg)	Vegetative growth
Juncus articulatus	Juncaceae	126	1	Herb	0.01	1
Juncus cognatus	Juncaceae	58	0	Herb	0.01	1
Juncus microcephalus	Juncaceae	60	0	Herb	0.01	1
Lantana camara	Verbenaceae	166	1	Shrub	18.40	2
Lonicera japonica	Caprifoliaceae	173	1	Climber	4.36	2
Lotus angustissimus	Fabaceae	94	0	Herb	0.54	2
Medicago lupulina	Fabaceae	110	0	Herb	0.72	1
Medicago polymorpha	Fabaceae	120	0	Herb	3.34	1
Melinis repens	Poaceae	115	1	Grass	0.22	2
Modiola caroliniana	Malvaceae	111	0	Herb	0.73	2
Nandina domestica	Nandinaceae	154	0	Shrub	27.16	2
Nassella trichotoma	Poaceae	109	1	Grass	0.33	1
Ochna serrulata	Ochnaceae	111	1	Shrub	25.55	1
Osteospermum ecklonis	Asteraceae	106	0	Shrub	32.37	1
Oxalis corniculata	Oxalidaceae	166	1	Herb	0.12	2
Paspalum dilatatum	Poaceae	116	1	Grass	1.50	2
Paspalum urvillei	Poaceae	98	0	Grass	0.58	2
Passiflora suberosa	Passifloraceae	97	1	Climber	4.58	2
Petrorhagia nanteuilii	Caryophyllaceae	121	0	Herb	0.15	1
Phalaris aquatica	Poaceae	124	1	Grass	1.27	2
Phytolacca octandra	Phytolaccaceae	122	0	Herb	4.88	2
Plantago lanceolata	Plantaginaceae	129	1	Herb	1.14	1
Poa annua	Poaceae	207	1	Grass	0.20	1
Polycarpon tetraphyllum	Caryophyllaceae	136	0	Herb	0.01	1
Psoralea pinnata	Fabaceae	120	0	Shrub	14.61	1
Richardia stellaris	Rubiaceae	120	0	Herb	0.36	1
Rubus ulmifolius	Rosaceae	171	0	Shrub	2.58	2
Senecio madagascariensis	Asteraceae	91	1	Herb	0.12	2
Sida rhombifolia	Malvaceae	129	1	Shrub	2.07	1
Solanum mauritianum	Solanaceae	114	1	Tree	1.16	2
Solanum nigrum	Solanaceae	207	1	Shrub	0.45	1
Solanum pseudocapsicum	Solanaceae	152	1	Shrub	3.09	1
Soliva sessilis	Asteraceae	110	0	Herb	0.36	2
Sonchus oleraceus	Asteraceae	206	1	Herb	0.26	1
Sporobolus africanus	Poaceae	199	1	Grass	0.23	1
Sporobolus fertilis	Poaceae	199	1	Grass	0.31	1
Stellaria media	Caryophyllaceae	129	1	Herb	0.27	1
Stenotaphrum secundatum	Poaceae	136	0	Grass	1.51	2
Taraxacum officinale	Asteraceae	143	0	Herb	0.63	1
Trifolium campestre	Fabaceae	111	0	Herb	0.18	1
Trifolium dubium	Fabaceae	132	0	Herb	0.38	1
Trifolium repens	Fabaceae	125	0	Herb	0.61	2
Trifolium striatum	Fabaceae	96	0	Herb	0.25	1

Table 1 continued

Species	Family	MRT	Status	Growth form	Seed mass (mg)	Vegetative growth
Verbena bonariensis	Verbenaceae	128	0	Herb	0.17	2
Verbena litoralis	Verbenaceae	107	0	Herb	0.22	1
Verbena rigida	Verbenaceae	145	0	Herb	0.30	2
Veronica arvensis	Plantaginaceae	118	0	Herb	0.59	1
Vulpia myuros	Poaceae	129	1	Grass	0.31	1

classified as invasive across Australia (category '5A' species). We used this source of information in conjunction with PIER (2009) to identify the invasive species in our dataset. Invasive species are those that have spread rapidly from maternal populations, often creating monocultures in the process, and are those that are often linked to high impacts on the environment (Randall 2007). All remaining naturalized species in the dataset were classified as non-invasive. The separation of species into two clearly defined categories, invasive species that are successful invaders and non-invasive species that are naturalized but which have not invaded successfully, allowed us to address explicitly the nature of the relationships between plant dispersal characteristics and the shift from the state of naturalization to the state of invasion.

As a final consideration in the assembly of our dataset, the minimum residence time of each species in Australia was determined (Table 1), measured as the current year 2009 minus the year of first record (data extracted from Hamilton et al. 2005). To minimise the effects of residence time on invasiveness (i.e., longer residence times are linked to the likelihood of becoming invasive, see Pyšek and Jarošík 2005), and to ensure that any significant trait correlations with invasiveness were not confounded with residence time, invasive and non-invasive species were only included in the dataset if their presence in Australia exceeded a time period of more than 50 years. Although it is difficult to assign an exact period after which species will have become invasive in a region, this is roughly the length of time required for sleeper weeds to 'awaken' and become invasive (Groves 2006). It is worth noting, however, that over 90% of our study species were introduced to Australia more than 90 years ago (Table 1) and a comparison of minimum residence times between invasive and non-invasive species in our dataset

revealed no significant difference (one-way ANOVA, $F_{1,86} = 3.75$, $P > 0.05$).

Plant trait data

Diaspores (seeds plus dispersal structures) were obtained for each species from mature plants growing in Royal National Park. A total of twenty diaspores, each from a different individual plant, were collected for each species. Dispersal structures including wings, hairs, hooks, and fleshy fruit were separated from seeds to determine what proportion of the total diaspore mass represented dispersal investment (Edwards and Westoby 1996). Mean seed mass and dispersal structure mass were determined by individual weighing using a Cahn 29 microbalance. The primary dispersal mode of each species was classified as either anemochory (wind-dispersed seeds with wings or hairs), exozoochory (seeds with hooks dispersed by adhesion to animals), autochory (seeds dispersed ballistically by a specialized capsule), endozoochory (seeds within a fleshy fruit) or as unassisted.

We included three plant traits as control variables in our analyses (see statistical analysis section below). We controlled for seed mass (measurements described above) because it is known to be linked to invasion success in exotic plants at a landscape scale in Australia (Hamilton et al. 2005). We classified species as either a grass, herb, shrub, tree or climber and also classified species based on observed capacity for vegetative spread (Fairley and Moore 1995; Harden 1990–1993; Botanic Gardens Trust 2009). We controlled for growth form to ensure that comparisons of dispersal investment among plants such as trees, grasses and climbers were meaningful. Because it may be argued that investment in seed dispersal may be more important in species that are not capable of vegetative dispersal and growth, we

also controlled for capacity for vegetative spread to ensure that it was not confounding relationships between dispersal investment and invasiveness.

Statistical analysis

We used generalized linear models to analyse our dataset (GLIM version 3.77, Royal Statistical Society, London). Categorization of species as non-invasive or invasive was the response variable in all analyses, thus a binomial error structure with a logit link was employed in binary logistic regressions for cross-species analyses (Crawley 1993). Cross-species regressions did not explicitly consider phylogenetic relatedness among species. A second analysis that explicitly considered phylogenetic relatedness among species was performed (Harvey and Pagel 1991). Independent contrasts analysis was carried out by implementation of the phylogenetic regression in GLIM (Grafen 1989). Such regression models require the construction and coding of a phylogeny. A phylogenetic tree describing the hypothesized evolutionary relationships between species was constructed using Phylomatic software (Webb and Donoghue 2005). Phylomatic employs a backbone family-level tree of the angiosperms based on a synthesis of recent phylogenetic analyses. After a list of the study species has been entered into the Phylomatic software, the appropriate families are selected from the backbone structure and the remainder pruned from the tree, with genera generally pasted on as polytomies within families and species as polytomies within genera (e.g., Wright et al. 2007). The affinity of one species, *Nandina domestica* (Nandinaceae), was uncertain, and as a consequence it was grafted onto the phylogenetic tree at the lowest node where affinity was certain. This is the most conservative manner of incorporating such groups into a working phylogeny (Murray et al. 2002). Each node in the constructed phylogenetic tree contributed one independent data point (contrast) in the analysis. The 'default method' was used in phylogenetic regression models, and path segment lengths for the phylogenetic tree were calculated by assigning a height to each node that was one less than the number of species below or on that node in the tree (Grafen 1989). Plant life-history traits were entered into models as either continuous (dispersal investment, seed mass) or categorical (dispersal mode, growth

form, capacity for vegetative spread) explanatory variables. Prior to analyses, dispersal investment data were arcsine square root transformed and seed mass data were log transformed to approach normality and ensure homogeneity of variances.

Our analyses were performed in two consecutive stages. First, we built single-variable regression models to quantify pair-wise relationships between invasion status and dispersal investment as well as invasion status and dispersal mode. We then performed multiple regressions to examine the performance of each dispersal trait as an explanatory variable after accounting for the separate effects of plant growth form, seed mass and capacity for vegetative growth, as well as accounting for the combined effects of all three of these trait variables. We considered each dispersal trait separately in multiple regression analyses given the strong correlation between the two traits ($r = 0.87$, $P < 0.0001$), which can lead to unstable parameter estimates if both are included in multiple regression models (Crawley 2007). In multiple regression analysis, we determined variation in the response variable accounted for by each dispersal trait over and above the effects of the other explanatory variables in the model (Norman and Streiner 2000). For instance, we were able to determine whether dispersal investment was capable of explaining significant variation in invasion success independently of growth form, seed mass and capacity for vegetative growth.

Results

Dispersal investment was significantly related to invasion success in both cross-species and phylogenetic regressions (Tables 2, 3), with invasive species investing comparatively more in dispersal appendages than non-invasive species (Fig. 1). The relationship between dispersal investment and invasion success was still significant after controlling separately for the effects of growth form, seed mass and capacity for vegetative growth and when all three of these traits were controlled for simultaneously in cross-species analyses (Table 2), as well as in independent contrasts analyses, albeit marginally ($P = 0.05$) when all traits were controlled for (Table 3).

Table 2 Cross-species relationships between invasion success (response variable) and (i) dispersal investment and (ii) dispersal mode (explanatory variables)

Control variables	(i) Dispersal investment			(ii) Dispersal mode		
	CD	df	P	CD	df	P
No control	10.29	1	0.001	15.71	4	0.003
Growth form	4.28	1	0.039	8.72	4	0.069
Seed mass	7.78	1	0.005	12.23	4	0.016
Vegetative growth	9.49	1	0.002	14.91	4	0.005
All control	4.30	1	0.038	8.63	4	0.07

Single-variable binary logistic regressions examined the pairwise relationship between invasion status and either dispersal investment or dispersal mode (no control). Multiple-variable binary logistic regressions controlled for the separate effects of plant growth form, seed mass and capacity for vegetative growth, as well as the combined effects of all three control variables (all control)

CD refers to the change in deviance resulting from the addition of either dispersal investment or dispersal mode to models. Changes in deviance were tested for significance against a χ^2 distribution

Table 3 Phylogenetic regressions between invasion success (response variable) and (i) dispersal investment and (ii) dispersal mode (explanatory variables)

Control variables	(i) Dispersal investment			(ii) Dispersal mode		
	F	df	P	F	df	P
No control	7.95	1, 34	0.008	2.61	4, 31	0.05
Growth form	4.00	1, 39	0.05	1.71	4, 36	0.17
Seed mass	8.06	1, 51	0.007	2.73	4, 48	0.04
Vegetative growth	8.50	1, 44	0.006	2.72	4, 41	0.04
All control	3.92	1, 46	0.05	1.77	4, 43	0.15

Single-variable regressions examined the pair-wise relationship between invasion status and either dispersal investment or dispersal mode (no control). Multiple-variable regressions controlled for the separate effects of plant growth form, seed mass and capacity for vegetative growth, as well as the combined effects of all three control variables (all control)

Although dispersal mode was significantly related to invasion success in a single-variable regression, the relationship disappeared after controlling for the effects of growth form, seed mass and capacity for vegetative growth in cross-species and independent contrasts analyses (Tables 2, 3). Controlling for each of these variables separately indicated that the significance of dispersal mode disappeared after taking into
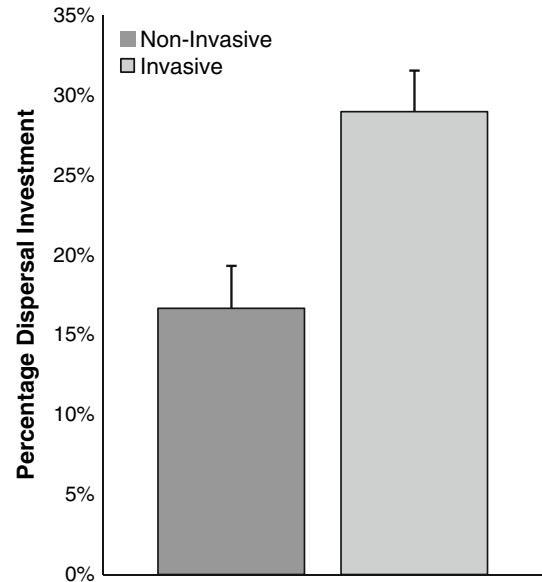
Fig. 1 The average percentage investment in dispersal appendages ($\pm$SE) for the pools of non-invasive and invasive species in the study region
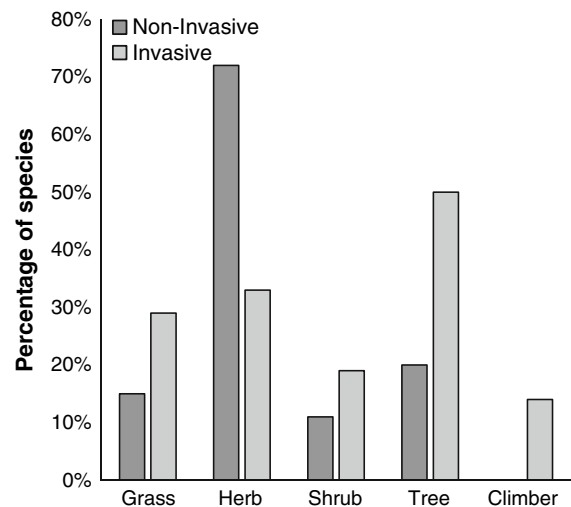
Fig. 2 The percentage of invasive and non-invasive exotic plant species in the study region in each primary growth form

account the effects of growth form, but not seed mass or vegetative spread (Table 2). The relationship between dispersal mode and invasion success was thus a secondary correlate as a result of a significant relationship between dispersal mode and growth form ($\chi^2 = 58.90$, $df = 16$, $P < 0.0001$) and growth form and invasion status ($\chi^2 = 18.41$, $df = 14$, $P < 0.01$), with invasive species more likely to be grasses, shrubs,
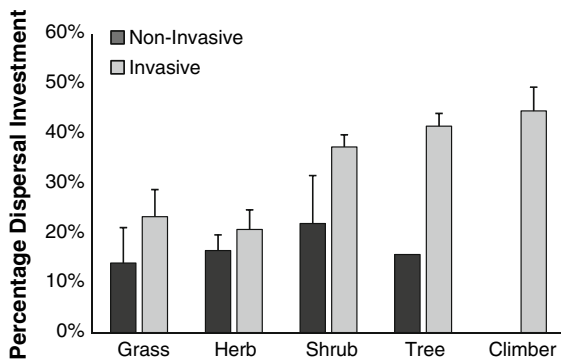
Fig. 3 The percentage investment in dispersal appendages (±SE) of invasive and non-invasive exotic plant species as a function of growth form

trees and climbers, but less likely to be herbaceous (Fig. 2). In this context, it is important to note that dispersal investment was significantly related to invasion success even after controlling for growth form (Fig. 3).

Discussion

Our results show that investment in seed dispersal structures is linked to invasiveness in exotic plants of south-eastern Australia. Exotic plant species that have become invasive in this region invest significantly more resources into dispersing their seeds than species that are not invasive. This finding supports the hypothesis that larger investment in seed dispersal structures leads to an increased chance of naturalized species dispersing their populations over considerable distances from sites of introduction and thus shifting from a naturalized state to an invasive one. Overcoming this dispersal barrier is paramount if naturalized species are to become invasive (Pyšek and Richardson 2008). Hanspach et al. (2008) indicate that research attempting to elucidate the factors underpinning invasion success should focus on a specific stage of the invasion pathway and compare species that successfully shift from one stage with species that do not make the transition. In the case of their study, they examined species that have shifted from being a casual introduction to becoming naturalized, to find that, among other traits relevant to that transition, winter hardiness was linked to naturalization success. In our study, we also focussed specifically on a particular stage of the invasion pathway,

the crucial stage of the shift from naturalization to invasion (e.g., Pyšek et al. 1995; Hamilton et al. 2005). By testing, with field-collected data, a specific dispersal-related hypothesis about the naturalization-invasion transition, we have shown that investment in seed dispersal structures is important for invasion success.

Although on first analysis, the mode with which seeds are dispersed appeared to be a significant correlate of invasiveness, our analyses that controlled for other plant traits that are either known to be important for invasion success in the exotic plants of the study region (e.g., seed mass, Hamilton et al. 2005) or that are known to be correlated with dispersal mode (e.g., growth form, Leishman et al. 1995), demonstrated that dispersal mode was not a primary correlate of invasion success. Other studies have shown that failure to account for the influence of life-history traits that have the potential to confound analyses can have severe ramifications (Murray and Hose 2005). Based on our findings, it is important to make a clear distinction between dispersal investment and dispersal mode in relation to invasion success. Higher investment in dispersal structures for seeds, regardless of the structures present on the seed that offer the mode of dispersal (e.g., wings versus fleshy fruits), is the key quantity of the two dispersal features for invasion success.

It is not surprising that dispersal mode was found not to be important in our study, as according to Pyšek and Richardson (2008), plant traits that are typically used to define dispersal capacity (e.g., morphology) are somewhat inappropriate for predicting the potential spread dynamics of alien species. We believe that in contrast to simply classifying species based solely on dispersal mode, measuring the actual amount of resources devoted to dispersing seeds does provide an appropriate test of dispersal potential (see also Edwards and Westoby 1996). Nevertheless, it will be important as a next step to measure dispersal distances (e.g., Cousens et al. 2008) to understand further the invasion process, although measurements of this sort are in some cases incredibly difficult to measure reliably given the importance of rare, long-distance dispersal events.

Some invasive species were found to invest a staggeringly large proportion of their total diaspore mass in dispersal structures (Table 1). For example, *Lonicera japonica*, *Hedera Helix* and *Acetosa*

sagittata invested between 60 and 70% in dispersal structures. Interestingly, these are all climbers, which reflects our finding for particular growth forms such as climbers to be more likely to be invasive among the species in our dataset. Such a high investment in dispersal features in this growth form is probably a reflection of the fact that they evolved to use host plants as structural support. As a consequence, climbers can invest a proportionately larger amount of resources in reproductive and notably dispersal features because they need not invest heavily in large stems for support. Because there is a general positive allometric relationship between seed mass and dispersal investment (Edwards et al. 2006), it might be argued that comparatively large seed mass in these species, rather than dispersal investment, is driving the observed relationship between dispersal investment and invasion success. Indeed, there is a significant positive correlation between seed mass and dispersal investment among the species in our dataset ($r = 0.34$, $P < 0.01$). This argument can be eliminated, however, because our analyses that controlled for both growth form and seed mass found that dispersal investment was still able to account for a significant and unique proportion of variation in invasion success.

One other study has explored the relationship between seed dispersal investment and plant species distribution patterns. Edwards and Westoby (1996) examined dispersal investment among native species of the Australian continent and found no overall tendency for widely distributed species to invest proportionately more heavily in dispersal structures than narrowly distributed species. The native species in the dataset of Edwards and Westoby (1996) have had a considerably longer time period in which to disperse, interact with other species and expand their ranges compared with the more recent exotic plant arrivals in Australia. The difference between their finding and ours is most likely because we focussed on a specific stage of the invasion pathway where dispersal investment is crucial for range expansion among a set of contemporary exotic invaders.

Our finding that growth form was a significant factor underlying invasion success among the study species of south-eastern Australia is somewhat consistent with a recent continental study of the naturalization to invasion pathway in Australia (Phillips et al. 2010). In that study, it was found that herbaceous species were less likely to be successful invaders across Australia. Our regional study provides some early support that there may be consistency across spatial scales in terms of a relationship between growth form (i.e., herbaceous form) and non-invasiveness. This consistency may be complicated, however, in analyses of growth form and invasiveness in regions dominated by agricultural systems, where herbaceous species are probably more likely to be among the more invasive poll of species.

At present, there are two approaches to performing research that investigates the links between plant traits and invasion success. Some studies build extremely large species databases (e.g., over 8,000 species in Bradshaw et al. 2008; Hanspach et al. 2008) and examine traits for which data are readily available in the literature (e.g., plant height, longevity). Other studies, such as the present one, focus on traits for which new field data need to be collected (e.g., Godfree et al. 2004; Bass et al. 2006). Necessarily, given time and logistical constraints, there is a trade-off between effort involved in the collection of fresh field data and the number of species that can be realistically examined in such studies. We made every effort to measure dispersal investment for all naturalized, seed-dispersing species in a large region of south-eastern Australia, given the constraints of accounting for residence time. Although not in the realm of 8,000 species, our study of close to 100 species (including all species of the region relevant to our hypothesis) has provided insight into the significance of seed dispersal investment for plant invasiveness. We suggest that the approach of using comparatively smaller datasets is just as important as studies that use large datasets of thousands of species. Both approaches have the potential to improve our fundamental understanding of biological invasions (Pyšek and Richardson 2007).

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