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Invasiveness in exotic plant species is linked to high seed survival in the soil

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ABSTRACT

Background: Exotic species often do no harm for many generations and then become invasive. The science of invasion ecology seeks to determine the nature or causes of this change. Among the possibilities is that soil-borne fungi play a significant role in reducing the potential for invasiveness in the introduced range.

Predictions: The seed survival of invasive species in the soil exceeds that of non-invasives. Seed survival, both in invasives and non-invasives, is higher in the presence of fungicide, but fungicide improves the seed survival of non-invasives more than that of invasives.

Methods: A common garden experiment under field conditions to compare seed survival in the soil between invasive and non-invasive exotic plant species. We contrasted seven congeneric pairs of invasive and non-invasive species. The species in each pair originated from the same donor continent, shared similar growth form, habitat occurrence, and residence times in Australia. The addition of fungicide was used as an experimental treatment.

Results: Seed survival was significantly higher in invasive species. The addition of fungicide improved seed survival. However, there was also a significant interaction: the fungicide treatment had a significantly stronger effect on the seed survival of non-invasive species. Seed mass differences between congeners did not provide a consistent, significant explanation of seed survival differences.

Conclusion: The seeds of invasive species are better equipped to survive in the soil than those of non-invasive species. Moreover, soil-borne fungi play a key role in the lower seed survival of non-invasive species.

Keywords: exotic plants, invasive species, naturalization to invasion, seed size, soil fungi.

INTRODUCTION

Only a subset of exotic species that establish naturalized populations in new regions spread widely to become invasive (Williamson and Fitter, 1996). Nevertheless, this subset of invasive exotic plant species often has significant environmental and socio-economic impacts (Pimentel *et al.*, 2005; Pyšek and Richardson, 2010; Vilà *et al.*, 2010, 2011). Understanding how exotic plant species shift from naturalization to invasion is vital for managing the spread of invasive species

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(Richardson *et al.*, 2000). One approach for understanding this shift is to identify plant functional traits that distinguish invasive from non-invasive species (Kolar and Lodge, 2001; Pyšek and Richardson, 2007; van Kleunen *et al.*, 2010). Previous work on invasive plants in Australia has shown that high specific leaf area and increased investment in seed dispersal structures lead to successful invasion (Hamilton *et al.*, 2005; Murray and Phillips, 2010). However, we are still a long way from completely understanding the mechanisms underpinning the successful spread of invasive plant species.

When exotic plants are introduced to new regions, their seeds are likely to encounter novel fungal species in the soil compared with the fungal flora of soils of their native ranges (Blaney and Kotanen, 2001). Indeed, soil-borne fungi are ubiquitous; within one gram of soil, several hundred metres of fungal hyphae can be found (Leake *et al.*, 2004). Interactions between germinating seeds and soil-borne fungi can have a range of effects in the context of plant invasions. A beneficial effect occurs when the growth of seedlings and adults of exotic plant species is promoted in the introduced range (compared with the native range) via successful, novel symbiotic mycorrhizal interactions (Marler *et al.*, 1999; Reinhart and Callaway, 2006). This might also involve release from particular soil pathogens in the native range [i.e. the enemy release hypothesis (Mitchell and Power, 2003; Torchin and Mitchell, 2004)]. In contrast, however, exotic plant seeds are also open to attack from pathogenic fungi (Blaney and Kotanen, 2002). It is widely documented that seeds in general often suffer high mortality rates in the soil, largely from pathogenic surface-contaminating fungi (Kirkpatrick and Bazzaz, 1979; Leck *et al.*, 1989; Keane and Crawley, 2002). Pathogenic fungi actively attach to a host plant and consume the nutrients from the plant, either by breaking down the living plant tissue using toxins and depolymerizing enzymes (Oliver and Ipcho, 2004), or by spreading throughout the living tissue and passively diverting nutrients away from the host plant (Glazebrook, 2005). Such destructive encounters have important implications for distinguishing between invasive and non-invasive species in the naturalization-to-invasion transition. For some exotic plant species, for instance, pathogenic fungi may act as an inhibitory barrier and prevent populations establishing and increasing to over-abundance at new sites in the introduced range due to seed mortality in the soil. In contrast, exotic plant species that produce persistent seed banks by surviving better the attacks of soil-borne fungi will have an edge in transitioning beyond a naturalized state to become invasive.

In the present study, we compared seed survival between invasive and non-invasive exotic plant species in a common garden experiment. We performed a seed burial experiment under field conditions and employed seven pairs of congeneric contrasts between invasive and non-invasive species. We sought to determine whether higher seed survival in the soil is found in the invasive species in each pair compared with the non-invasive species across the congeneric contrasts. The contrasts were selected such that the species in each pair originated from the same donor continent, shared similar growth form, habitat occurrence and residence times in Australia. We included the addition of fungicide as an experimental treatment. We tested the predictions that seed survival is higher in the presence of fungicide and that a larger increase in seed survival in the presence of fungicide should be observed in non-invasive species if soil-borne fungi play a significant role in reducing their potential for invasiveness in the introduced range. In addition, given that interspecific variation in seed mass has been linked to variation in seed bank longevity among species (Thompson *et al.*, 1993; Funes *et al.*, 1999), we measured the seed mass of each of our study species and included seed mass measurements as covariates in our analytical procedures. In this way, we could account for seed mass variation among species as a potential underpinning of seed survival.

METHODS

Invasive versus non-invasive congeneric contrasts

We compared seed survival between an invasive and a non-invasive exotic plant species in each of seven congeneric pairs of species (Table 1). Each congeneric pair was selected to allow a naturalized invader that has spread rapidly and widely in Australia to be contrasted with a non-invasive congener that has not been recorded as noxious or a weed of agriculture or the environment, and in spite of widespread ornamental or agricultural planting, has never been recorded as spreading invasively in Australia (Randall, 2007). We ensured that the invasive and non-invasive species in each contrast differed substantially in the extent of invasiveness across Australia, with geographic range sizes of non-invasive species being at least ten times smaller than the ranges of invasive congeners. Range size data [as area of occupancy (see Hamilton *et al.*, 2005)] were obtained from herbarium records maintained at Australia's Virtual Herbarium (http://avh.rbg.vic.gov.au/avh/; accessed July 2010).

Table 1. Invasive and non-invasive exotic plant species in each of the seven congeneric contrasts

Genus	Species	Family	Status	Origin	Growth form	Minimum residence time (years)
Aristolochia	*elegans*	Aristolochiaceae	Invasive	South America	Vine	113
Aristolochia	*grandiflora*	Aristolochiaceae	Non-invasive	South America	Vine	125
Coreopsis	*lanceolata*	Asteraceae	Invasive	North America	Herb	150
Coreopsis	*grandiflora*	Asteraceae	Non-invasive	North America	Herb	60
Lonicera	*japonica*	Caprifoliaceae	Invasive	Asia	Shrub	193
Lonicera	*fragrantissima*	Caprifoliaceae	Non-invasive	Asia	Shrub	108
Paspalum	*dilatatum*	Poaceae	Invasive	South America	Grass	134
Paspalum	*fasciculatum*	Poaceae	Non-invasive	South America	Grass	78
Passiflora	*foetida*	Passifloraceae	Invasive	South America	Vine	167
Passiflora	*coccinea*	Passifloraceae	Non-invasive	South America	Vine	167
Salvia	*coccinea*	Lamiaceae	Invasive	South America	Herb	159
Salvia	*splendens*	Lamiaceae	Non-invasive	South America	Herb	167
Solanum	*betaceum*	Solanaceae	Invasive	South America	Shrub	126
Solanum	*torvum*	Solanaceae	Non-invasive	South America	Shrub	80

Since long residence time is an important predictor of invasiveness in exotic plant species in Australia (Hamilton *et al.*, 2005; Harris *et al.*, 2007; Phillips *et al.*, 2010), both the invasive and non-invasives in each contrast were selected with similar residence times. Residence times in all species and contrasts were a minimum of 60 years (e.g. Murray and Phillips, 2010), a period of time that with current knowledge adequately covers short lag times from introduction to first evidence of invasive spread for plant species (Hobbs and Humphries, 1995; Daehler, 2009). Residence time for each species was calculated as the year of analysis (2011) minus the earliest year of introduction (Hamilton *et al.*, 2005). The Department of Agriculture, Fisheries and Forestry Census of Cultivated Plants 2009 provided data on the earliest year of introduction for each species.

Invasive and non-invasive species in each contrast were selected such that they originated from the same donor continent and were of the same growth form (data from Phillips *et al.*, 2010). Within each contrast, both species overlapped in range and co-occurred in habitat within Australia as, for our predictions, there was no logic in contrasting species from vastly different areas and habitats and thus potentially exposed to a different suite of environmental conditions. Co-occurrence information was sourced from a range of botanical records including the Flora of New South Wales online database PlantNet and congeneric species were matched by habitat using the IBRA bioregion classification (v.16.1), a system that provides information on differentiated regions within Australia that are defined using common environmental characteristics including geology, topology, climate, and plant and animal communities (Thackway and Cresswell, 1995).

Seed survival measurements

The seed burial experiment was performed as a common garden experiment in open canopy dry sclerophyll woodland on privately owned land at the Faulconbridge Ecological Research Station, in the Blue Mountains region of New South Wales (latitude 33°42′05″S, longitude 150°31′34″E, elevation 470 m), Australia. The area has low-nutrient, clay to sandy soil and receives an average of 200–300 mm of rainfall during the spring season and is typical of large tracts of native woodland throughout eastern Australia. All of the study species are known to grow in this woodland habitat and there are a multitude of pathways by which seeds from naturalized populations can disperse to these woodland locations. Our experiment explicitly asked, if seeds of invasive and non-invasive congeners reach the soil of woodland habitat at the same time, does the invasive species demonstrate higher seed survival than the non-invasive species?

Fresh seed of each of the study species was sourced from commercial seed suppliers from three naturalized populations within Australia. For each species, 30 seeds were weighed (to microgram precision on a LIBROR-AEL-160 electronic analytical balance, Shimadzu, Japan). Seed mass was measured prior to the experiment as the seed coat plus embryo and endosperm, with all dispersal structures removed before weighing. Seed bags used to contain the seeds in the soil during the experiment were constructed from a single nylon tough cloth with the outer seams sealed completely using stainless steel staples. Two replicate seed bags were used for each treatment combination. A 4×4 m grid was created at the study site, with 10 cm deep holes dug at 50 cm intervals along the grid. At each interval, one randomly selected seed bag was buried below the soil surface. Each bag was labelled and filled with 20 randomly selected seeds of a single species and a mix of 450 ml sieved field soil from the experimental study region and 50 ml fine-grade sterile vermiculite. Thus, each

bag contained only the seeds of one species. The small quantity of vermiculite was added to each bag to promote water diffusion through the cloth membrane to avoid seed desiccation. We selected 20 seeds to place in each seed bag to reflect realistic seed bank densities that might occur for the study species and also to prevent seed-to-seed contamination by pathogenic fungi, an effect that has been found to occur more readily with higher density seed treatments (van Mourik *et al.*, 2005).

All seeds used in the experiment were surface sterilized by inundating them in a 10% solution of sodium hypochlorite (NaOCl) for 10 min to remove any potential pre-existing pathogenic contamination that could bias the survival rates of seeds in the experiment. The seed bags were then put into one of two treatments: (1) control, seed bag saturated in water before burial, and (2) fungicide treatment, seed bag saturated in fungicide solution before burial. The fungicide treatment was a 1:100 solution of Captan fungicide (*N*-trichloromethylthio-4-cyclohexene-1, 2-dicarboximide) from 48.9% pure wettable powder. Captan is a non-systemic heterocyclic nitrogen fungicide used against a diverse range of fungi including *Botryis*, *Fusarium*, *Fusicoccum*, and *Pythium* (Sharvelle, 1961; Torgeson, 1969; Martinez *et al.*, 1998; Blaney and Kotanen, 2001), and has been noted for its efficacy against seed-rotting fungi (Neergaard, 1979). The seed bags were buried in the field at the beginning of the spring season (September 2009) early in the natural cycle of seed dispersal. After 12 weeks in the soil, all seed bags were excavated from the site and transported intact to the greenhouses at the University of Technology Sydney. The excavated seed bags were opened and the inner soil contents spread evenly over sterilized potting mix in pots ($95 \times 95 \times 90$ mm) and exposed to optimum temperature, light, and water conditions for an additional 3 months. Surface soil agitation was applied every 2 weeks to mimic natural disturbance and encourage deeper-buried seeds to germinate. A census of the total number of germinated seeds for each bag was performed at the end of the 3 month period. In a number of excavated bags, seeds had already germinated before greenhouse treatment; these germinated seeds were added to the total number of seeds that germinated in the greenhouse in the following months. All remaining seeds in each bag that had not germinated were decomposed to such a state as to be clearly dead with no further possibility of germination. Thus, we measured seed survival for each of the species as the number of seeds germinated from the 20 seeds in each replicate for each of the two experimental treatments.

Statistical analysis

We modelled variation in seed survival in relation to explanatory variables using generalized linear mixed models with the function glmer (library lme4) in the R package v.2.14.2011-10-24 (R Development Core Team, 2005). Variation in seed survival (the response variable) was modelled as a function of invasive status (a fixed factor, invasive or non-invasive), genus (a random factor, membership in one of seven genera), fungicide treatment (a fixed factor, fungicide added or control with no fungicide), and the continuous covariate seed mass (ln-transformed prior to analysis). We specified a binomial error structure with a logit link in models as seed survival was measured in the form of proportion data. The use of a binomial error structure can provide analytical outcomes that are more difficult to interpret than the use of normal errors if the sample size is small. Our analysis, however, used an acceptably large (> 30) number of samples (Crawley, 2007).

Our aim was to build a minimum adequate model to explain variation in seed survival (Crawley, 2007). The full model was fitted first, which included the covariate seed mass and the

main effects of invasive status, genus and fungicide treatment, and all two-way and the three-way interactions. We then began the process of model simplification by inspecting the parameter estimates (using Wald Z-tests) and removing the least significant terms starting with the highest-order interactions. After the removal of a term from the model, we compared the initial and reduced models using Akaike's Information Criterion (AIC). If the reduced model had a lower AIC value than the initial model, the term was left out and we continued the process of model simplification. To compare models with different structures, we switched from the Restricted Maximum Likelihood Method to the Maximum Likelihood Method when comparing AIC values (Bolker *et al.*, 2009). We also used log-likelihood ratio tests to test the significance of the change in deviance resulting from the removal of random factors and the covariate during model simplification. Once the minimum adequate model was identified, we checked for over-dispersion, which occurs when there is more variability around a model's fitted values than is consistent with a binomial formulation. To do this, we fitted an observation-level random effect to the model. This factor had zero variance in the model and hence our model was not over-dispersed.

RESULTS

The model simplification procedure produced a minimum adequate model that retained several explanatory variables linked to seed survival. There was a highly significant main effect of invasion status on seed survival such that seed survival was higher in the invasive species (parameter estimate = 1.97, S.D. = 0.42, $Z = 4.69$, $P < 0.001$; Fig. 1a). There was also a significant main effect of fungicide treatment on seed survival, with seed survival higher in seeds treated with fungicide (parameter estimate = 0.54, S.D. = 0.21, $Z = 2.53$, $P < 0.05$; Fig. 1b). These main effects were superseded by a significant interaction between these fixed factors such that fungicide treatment improved seed survival in general but there was a noticeably stronger effect observed in non-invasive species (parameter estimate = 0.71, S.D. = 0.30, $Z = 2.39$, $P < 0.05$; Fig. 1c). Removal of two random factors during model simplification produced significant changes in deviance, thus genus ($\chi^2 = 5.60$, d.f. = 1, $P = 0.02$; variance = 1.32, S.D. = 1.55) and the genus × invasion status interaction ($\chi^2 = 22.17$, d.f. = 1, $P < 0.0001$; variance = 0.44, S.D. = 0.66) were retained in the final model. The genus × invasion status interaction arose because seed survival was significantly higher in invasive compared with non-invasive species within six of the seven congeneric pairs, including *Aristolochia*, *Coreopsis*, *Lonicera*, *Paspalum*, *Passiflora*, and *Salvia*, but not in the remaining contrast *Solanum* (Fig. 2). A key finding from model simplification was that removal of the covariate seed mass resulted in a non-significant change in deviance and thus it was not retained in the minimum adequate model ($\chi^2 = 0.51$, d.f. = 1, $P = 0.48$). In fact, seed mass differences between invasive and non-invasive species varied among the pairs, such that seeds were heavier in some contrasts and smaller in others (Fig. 3).

DISCUSSION

We found an important link between invasiveness in exotic plant species and higher seed survival in the soil. Our findings support the notion that seed survival in the soil plays a key role in facilitating the transition from naturalization to invasion. Importantly, our modelling showed that higher seed survival in invasive species was not mediated by interspecific variation in seed mass. Indeed, in phylogenetically independent contrasts

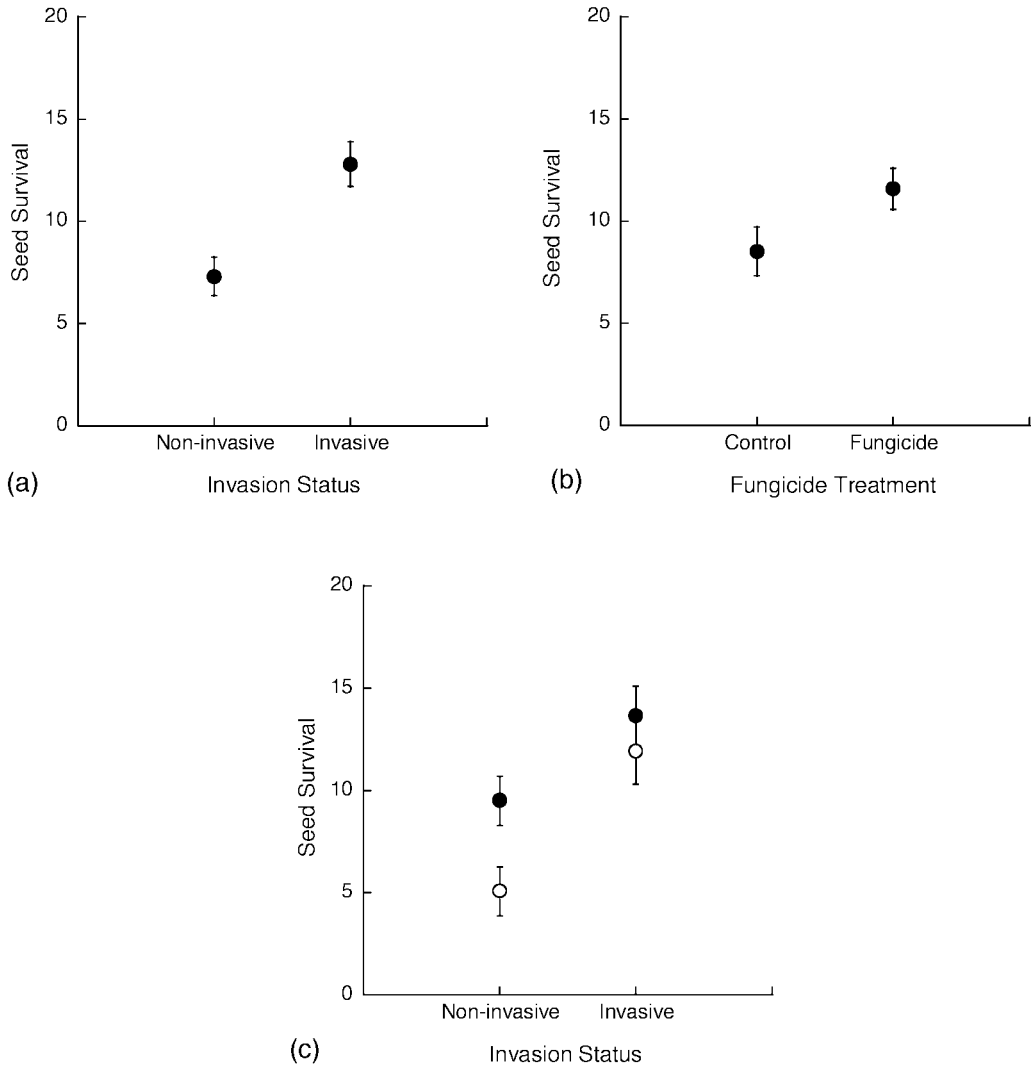

Fig. 1. Comparison of mean seed survival (±S.E.) between (a) invasive and non-invasive species, (b) control group (no fungicide) and treatment group (fungicide addition), and (c) invasive and non-invasive species separated into the control (○) and treatment (●) groups.

(PICs) where seed survival was higher in the invasive species, both larger seed mass (e.g. *Lonicera*) and smaller seed mass (e.g. *Aristolochia*) were found in the invasive species (Fig. 3). A broad mechanistic explanation of higher seed survival in the invasive species therefore cannot be based on large or small seed size facilitating seed survival in the soil.

We found that seed survival was higher in the presence of fungicide in general and that a larger increase in seed survival in the presence of fungicide was observed in the non-invasive species. These findings suggest the presence of soil-borne fungi can limit the survival of seeds of exotic plant species in an introduced range, and importantly, the larger effect observed in non-invasive compared with invasive species means that fungal pathogens in the

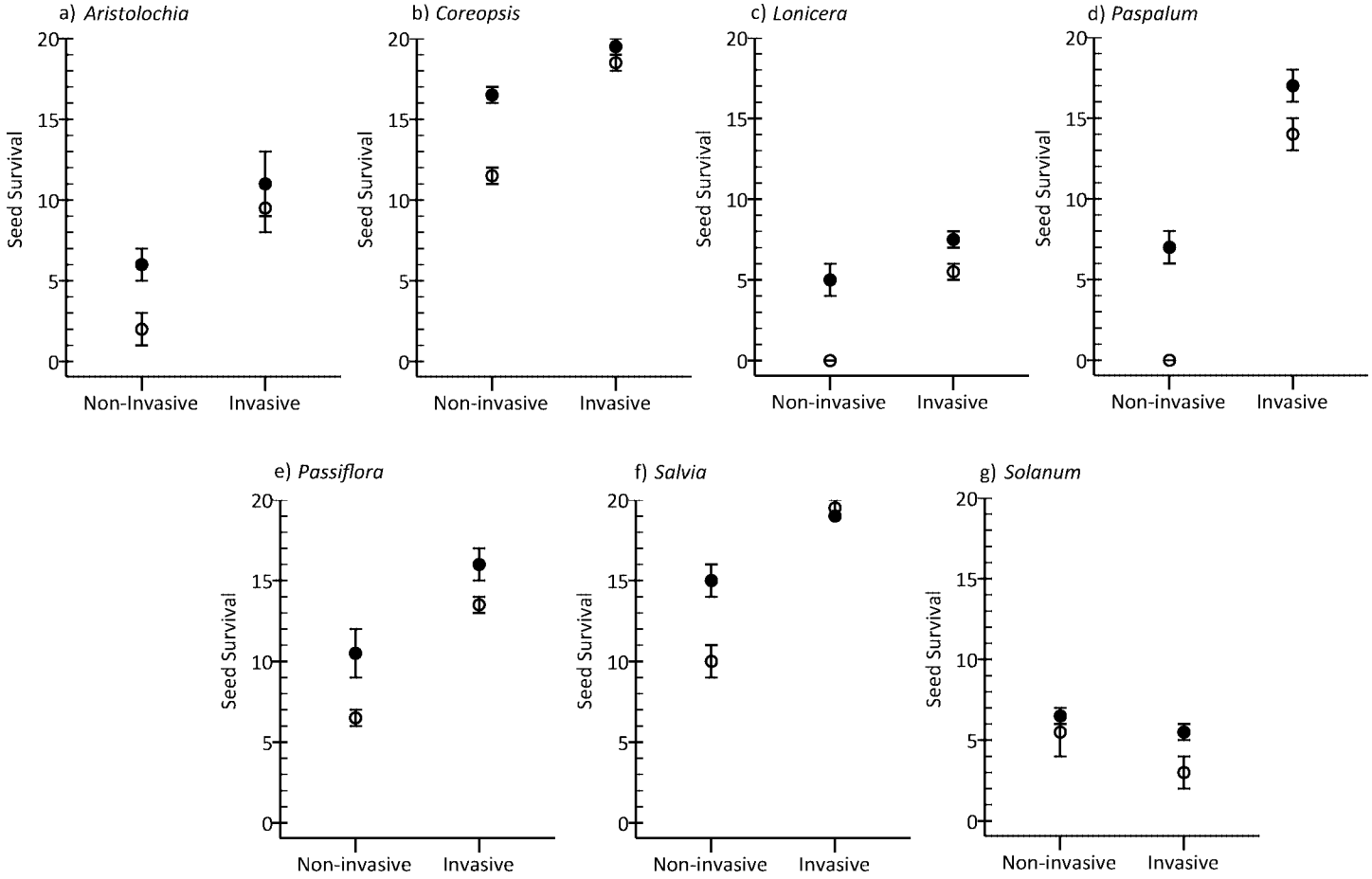

Fig. 2. Comparison of mean seed survival (± S.E.) between the invasive and non-invasive species of each congeneric contrast, separated into the control (○) and treatment (●) groups.

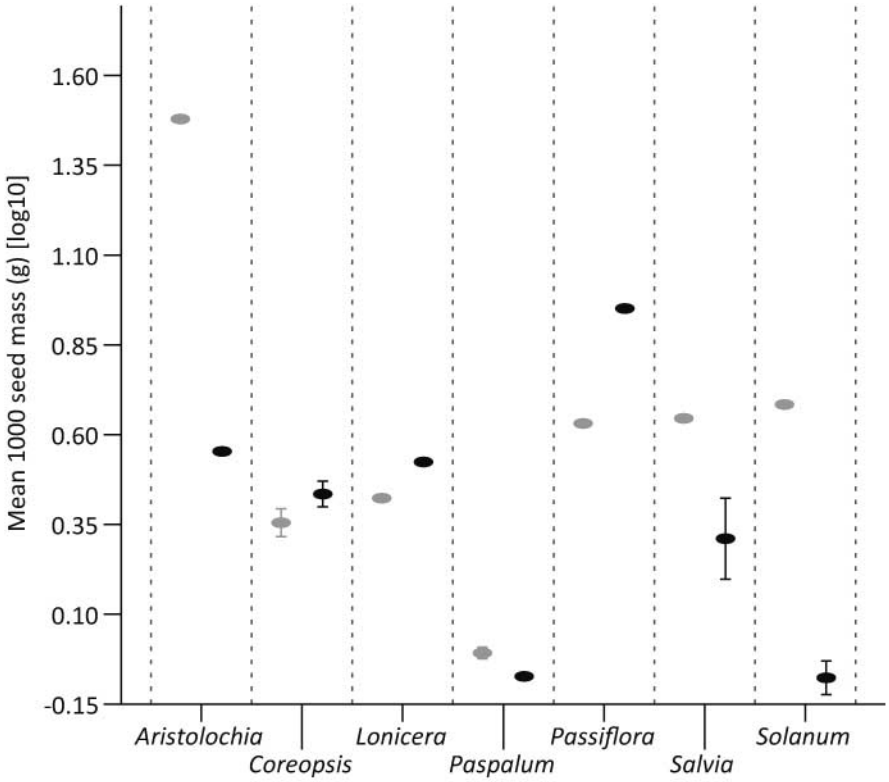

Fig. 3. Comparison of mean seed mass (± S.E.) between the invasive (solid ovals) and non-invasive (grey ovals) species of each congeneric contrast.

soil could play a significant role in reducing the potential of non-invasive species for invasive spread. Although soil-borne pathogenic fungi have often been attributed to increasing seed mortality during the seed bank phase (Kirkpatrick and Bazzaz, 1979; Leck *et al.*, 1989; Keane and Crawley, 2002), our study is the first to provide evidence of this interaction providing a mechanistic explanation of limitations to invasiveness in exotic plant species. Of note, seeds of two non-invasive plant species (*L. fragrantissima* and *P. fasciculatum*) were only able to survive in our experiment in the presence of fungicide, a finding which suggests that these two non-invasive species in particular are highly sensitive to soil-borne pathogens.

The genus *Solanum* provided the only exception to the pattern for higher seed survival in invasive species. Previous work investigating survival of seeds of members of the Solanaceae family against pathogenic attack has revealed that many genera and species of the family have anti-microbial, low-molecular-weight secondary metabolites (sesquiterpenoid phytoalexins) present in their tissues. These metabolites act as a protective agent against pathogenic interference including pathogenic soil fungi (Kuc, 1995). The production of this anti-microbial metabolite by both non-invasive *Solanum torvum* and invasive *Solanum betaceum* might have resulted in their similar levels of seed survival. However, these two species had the lowest seed survival across the PICs, which suggests that these species might not have been afforded the protection of anti-microbial metabolites. Indeed, studies have shown that initial production of phytoalexins by not-yet germinated

seed tissues is dependent on the occurrence of prolonged high soil moisture levels (Halloin, 1983). The dry Australian climate and the sandy soils of the study site, which do not hold moisture well, may have led to an absence of this important protective metabolite. This would have caused the seeds of both Solanaceaous species to be more susceptible to pathogenic attack.

Another factor that might have contributed to the invasive species demonstrating higher seed survival than the non-invasive species relates to properties of the seed coat. The physical and chemical composition of a seed ultimately governs both its susceptibility to predation by invertebrates, including ants, millipedes, isopods and earthworms (Baskin and Baskin, 1998; Eisenhauer *et al.*, 2009), and decomposition due to environmental intolerance of frost as well as damp conditions. Seeds with better physical and chemical adaptations to protect against these antagonistic processes will be able to survive longer in the soil (Halloin, 1983). These factors remain to be tested for our study genera, and their examination will add important information to the central findings of the research presented in this paper.

Studies such as ours, with a focus on plant functional traits for which further field data need to be collected over time using manipulative experimentation, reflect a trade-off between the effort involved in the collection of fresh field data and the number of species that can be realistically examined in such studies (e.g. Perglová *et al.*, 2009; Grotkopp *et al.*, 2010). These sorts of studies, which involve rigorous protocols for species selection in an evolutionary context (i.e. congeneric contrasts), combined with informative studies using extremely large (i.e. hundreds to thousands of species) databases involving traits for which data are readily available in the literature (Castro *et al.*, 2005; Herron *et al.*, 2007; Küster *et al.*, 2008; Hejda *et al.*, 2009; Pyšek *et al.*, 2009; Murray and Phillips, 2010), are crucial in our efforts to identify plant functional traits that explain invasiveness in exotic plant species. Both approaches have the potential to improve our fundamental understanding of biological invasions (Pyšek and Richardson, 2007). In our field setting, we were able to demonstrate that under similar conditions the seeds of invasive species are better equipped to survive in the soil than non-invasive species, providing experimental evidence for a naturalization-to-invasion advantage in invasive exotic plant species.

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