RESEARCH ARTICLE

Native fruit traits may mediate dispersal competition between native and non-native plants

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Abstract

Seed disperser preferences may mediate the impact of invasive, non-native plant species on their new ecological communities. Significant seed disperser preference for invasives over native species could facilitate the spread of the invasives while impeding native plant dispersal. Such competition for dispersers could negatively impact the fitness of some native plants. Here, we review published literature to identify circumstances under which preference for non-native fruits occurs. The importance of fruit attraction is underscored by several studies demonstrating that invasive, fleshy-fruited plant species are particularly attractive to regional frugivores. A small set of studies directly compare frugivore preference for native vs. invasive species, and we find that different designs and goals within such studies frequently yield contrasting results. When similar native and non-native plant species have been compared, frugivores have tended to show preference for the non-natives. This preference appears to stem from enhanced feeding efficiency or accessibility associated with the non-native fruits. On the other hand, studies examining preference within existing suites of co-occurring species, with no attempt to maximize fruit similarity, show mixed results, with frugivores in most cases acting opportunistically or preferring native species. A simple, exploratory meta-analysis finds significant preference for native species when these studies are examined as a group. We illustrate the contrasting findings typical of these two approaches with results from two small-scale aviary experiments we conducted to determine preference by frugivorous bird species in northern California. In these case studies, native birds preferred the native fruit species as long as it was dissimilar from non-native fruits, while non-native European starlings preferred non-native fruit. However, native birds showed slight, non-significant preference for non-native fruit species when such fruits were selected for their physical resemblance to the native fruit species. Based on our review and case studies, we propose that fruit characteristics of native plant communities could dictate how well a non-native, fleshy-fruited

plant species competes for dispersers with natives. Native bird preferences may be largely influenced by regional native fruits, such that birds are attracted to the colors, morphology, and infructescence structures characteristic of preferred native fruits. Non-native fruits exhibiting similar traits are likely to encounter bird communities predisposed to consume them. If those non-natives offer greater fruit abundance, energy content, or accessibility, they may outcompete native plants for dispersers.

Introduction

Invasive non-native plant species may exert a range of impacts on native communities. They can alter resource availability (e.g., Yelenik et al. 2004), transform fire regimes (Brooks et al. 2004), promote erosion (D'Antonio and Meyerson 2002), or reduce local diversity through formation of monodominant stands (Hejda et al. 2009, Greene and Blossey 2011). Additionally, invasive plant species may directly compete with natives by sequestering necessary resources such as water (e.g., Enloe et al. 2004) or nutrients (Wardle et al. 1994).

Competition with invasive plants may further impact native communities by altering interactions between native species. Invaders can transform food web structure, for example, by outcompeting high-quality native food plants and thereby diminishing an herbivore's resources (Going and Dudley 2008). Similarly, competition with invasives can disrupt mutualistic interactions, as when a non-native species monopolizes pollination services, diminishing native plant reproduction (Brown et al. 2002, Muñoz and Cavieres 2008). A number of authors have suggested that such competition may also derail native seed dispersal relationships (Vilá and D'Antonio 1998, Renne et al. 2000, Richardson et al. 2000, Gosper 2004, Traveset and Richardson 2006). However, dispersal competition has rarely been directly measured. It is unknown whether such competition is a widespread or significant impact of biological invasions.

Among introduced species, fleshy-fruited plants adapted to animal-mediated seed dispersal are often considered high-risk for invasiveness (Rejmánek and Richardson 1996, Daehler et al. 2004, Richardson and Rejmánek 2011). Along with enabling rapid spatial spread, zoochorous dispersal may enhance seed germination (Panetta and McKee 1997, Verdú and Traveset 2004) and disproportionately deposit seeds in favorable microsites (Wenny 2001). Notable invasions mediated by regional frugivores have included the tropical, monotypic stand-forming invaders *Lantana camara* (Gosper and Vivian-Smith 2006) and *Miconia calvescens* (Meyer 1998), the temperate forest invader *Lonicera mackii* (Schierenbeck 2004, Bartuszevige and Gorchov 2006), and the riparian specialist *Triadica sebifera* (Renne et al. 2002). The importance of animal-mediated dispersal in biological invasions has been addressed in a number of

review papers (Richardson et al. 2000, Reichard et al. 2001, Daehler 2003, Gosper et al. 2005, Buckley et al. 2006, Schupp 2011, Tsoar et al. 2011).

Animal-dispersed invasive plants can have the same community impacts as other invasives, forming monospecific thickets (Williams et al. 2006), altering nutrient regimes (Cameron and Spencer 1989), and reducing the quality of wildlife habitat (Schmidt and Whelan 1999). If such species also monopolize seed dispersal services and quantitatively reduce native seed dispersal, they are likely to exert a competitive impact on native fleshy-fruiting plants, which may experience reduced fitness if their seeds fail to disperse from the immediate parent neighborhood (Ridley 1930, Liu et al., in press). An important component of this scenario is seed disperser preference: if dispersers commonly prefer invasive fruits, a significant reduction in dispersal of native species is likely (Gosper et al. 2006). Of course, frugivores do not explicitly consider a food plant's origin in their selection. However, non-native species could be particularly attractive to dispersers if they are relatively robust, with brightly-colored fruits, or exhibit very large crop sizes, all characteristics that might result from anthropogenic selection for horticultural purposes or from absence of natural enemies in the zone of introduction. On the other hand, dispersers may be more likely to favor native fruit species if they have natal experience with the fruits typical of the region (Stamps and Davis 2006) or if they display neophobia toward novel food items (Marples and Kelly 1999, Greenberg and Mettke-Hofmann 2001). If these scenarios are the rule, native fleshy-fruiting species might outcompete introduced species for dispersal, or at least are unlikely to be negatively impacted by dispersal competition, limiting the broad importance of such competition in biological invasions.

There have been a few attempts in localized systems to determine whether competition for dispersers occurs. Gosper et al. (2006) examined vertebrate-mediated dispersal of native plant species growing with and without invasive *Chrysanthemoides monilifera*, but found no effect of the invasive on native dispersal. Lichstein et al. (2004) found that native tree sapling mortality was elevated by *Ligustrum lucidum* invasion, but found no evidence that the invasive created dispersal limitation for natives. Similarly, although Aslan (2011) demonstrated potential competition for dispersers through niche overlap between native and non-native species in California, the native plant species in that system received proportionally more dispersal than did any of the non-natives. It is therefore unclear whether or not competition for dispersers is a common impact of biological invasions, or, rather, an unfounded suggestion by ecologists.

Since preference may play a key role in such competition, we combined a literature review, exploratory meta-analysis, and two case study aviary experiments to address the question: Under what circumstances do seed dispersers demonstrate preference for non-native fruits? We began by examining a number of studies that have probed the causes of fleshy-fruited invasion and identified characteristics that appear to promote animal-mediated dispersal of the invasive species in question. These studies do not directly compare native and non-native seed dispersal, but shed light on factors that may be pivotal in seed disperser preference. Additionally, a limited number of studies have directly examined frugivore preference for native vs non-native fruits

(Table 1). These studies have fallen into two categories: a small set of experiments comparing disperser preference for native and non-native species selected for their similarity; and somewhat more numerous studies comparing disperser preference for native and non-native species in an existing suite of co-occurring species, with no attempt to control species similarity. We conducted a small-scale meta-analysis on comparative studies containing sufficient quantitative information to examine relative disperser preferences for non-native vs. native species. Implications of resulting preference data varied qualitatively depending on study category. We illustrate the contrasting outcomes of the two approaches by including here the results of two aviary case studies we conducted in which we compared bird preferences for native and non-native species when fruits were controlled for similarity and when they were not. In combination, our review and case studies suggest that the regional native fruit assemblage is likely to strongly influence frugivore preferences, and that the degree to

Table 1. Studies that have directly compared seed disperser preferences for native vs. non-native fruits. Effect size, used in meta-analysis calculation, is the natural log of the response ratio, calculated as the proportion of non-native fruit consumed to the proportion of native fruit consumed. Studies with insufficient quantitative data were not included in the meta-analysis, although their qualitative results are discussed in the review. *Superior feeding efficiency* reflects author interpretations within each study and may include factors such as larger fruit size, higher fruit energy or nutritional content, higher fruit flesh to seed ratio, larger infructescences, larger plants, and more accessible fruits. † *Approach* distinguishes between studies that deliberately matched surface fruit characteristics such as color and fruit type (= "matched") and studies that examined existing suites of fruits without controlling for similarity (= "unmatched").

Study	Disperser	Effect size (lnRR)	Offers superior feeding efficiency
Approach †: Unmatched			
Corlett 2005	Birds	Insufficient quantitative data	Non-native
Drummond 2005	Birds	-0.06	Native
Ferreras et al. 2008	Birds	Insufficient quantitative data	Native
Greenberg and Walter 2010	Birds	0.04	No clear superior
Jung 1992	Birds	0.14	No clear superior
Meisenburg 2007	Birds	-0.12	Not discussed
Montaldo 2000	Birds	-0.20	Not discussed
Rowles and O'Dowd 2009	Ants	-0.33	Non-native
Whelan and Willson 1994	Birds	-0.82	No clear superior
White and Stiles 1992	Birds	Insufficient quantitative data	Native
Williams and Karl 1996	Birds	Insufficient quantitative data	Native
Our experiment #1, this paper	Birds	-0.62	No clear superior
Approach †: Matched			
Greenberg et al. 2001	Birds	-0.14	Not discussed
Jones and Wheelwright 1987	Birds	-1.84	Native
LaFleur et al. 2007	Birds	0.95	Non-native
Sallabanks 1993a	Birds	Insufficient quantitative data	Non-native
Our experiment #2, this paper	Birds	0.42	Not explored

which an introduced species monopolizes dispersal services may depend on its superficial similarity to native species.

Plant trait focus: Disentangling causes of ongoing fleshy-fruited plant invasions

Many studies in invasion biology are intended to elucidate the causes of ongoing invasions by particular species. Among fleshy-fruited invaders, fruit attractiveness to frugivore dispersers is frequently examined. Characteristics such as color, fruit size, infructescence structure, nutritional content, and pulp to seed ratio are considered general determinants of fruit attractiveness to frugivores (Debussche and Isenmann 1989, Herrera 1998, Levey and Martínez del Rio 2001, Sallabanks 1993b, Whelan and Willson 1994), and these traits have also been implicated in frugivore mediation of invasions (Westcott and Fletcher 2011). Larger fruit size may enhance feeding efficiency but can constrain dispersal if native frugivore gape widths are exceeded. Frugivores in Hong Kong consumed exotic fruits that were on average larger and contained relatively lower seed mass than native species (Corlett 2005), presumably boosting feeding efficiency. Similarly, cassowaries (*Casuarius casuarius*) in Australia demonstrated disproportionately high consumption of large-fruited species (Bradford et al. 2008). By contrast, *Asparagus asparagoides* is more invasive than *A. declinatus* in Australia although both are non-native: not only does *A. asparagoides* have brighter and more accessible displays than *A. declinatus*, but the smaller fruit size of *A. asparagoides* facilitates a wider array of potential frugivores due to gape width limitations (Bass et al. 2006). Smaller fruit sizes similarly enabled a substantially expanded suite of potential dispersers of *Olea europaea* fruits in California (Aslan and Rejmánek, in press) and in the Mediterranean (Rey et al. 1997) and promoted black rat dispersal of various non-native seeds in Hawaii (Shiels 2011). Fruit composition is also important. *Acacia cyclops*, a bird-dispersed invader in South Africa, produces arils that are much more energy-rich than those produced by non-bird-dispersed congeners (Glyphis et al. 1981). Within a broad array of native and invasive fleshy-fruiting species from the island of Mahé, invasive species exhibit a wider range of nutrient content than is found among natives and include many species nutritionally superior to any native species, suggesting that fruit energy content may aid plant invasions on oceanic islands (Kueffer et al. 2009). By contrast, bird-dispersed non-native species in New Jersey were found to be disproportionately low in nutritional quality and, perhaps as a consequence, consumed largely after native fruiting species were no longer available (White and Stiles 1992). Both within and between fruiting species, total per-tree crop size was significantly and positively related to bird visitation rates in some studies (Sallabanks 1992, Deckers et al. 2007), although it had no effect in others (Renne et al. 2000, Cordeiro et al. 2004, Aslan 2011, Greenberg et al. 2001). Crop size may be key in plant invasiveness in South Africa, where the fruiting displays of invasive non-native species tended to be larger and more conspicuous than those of native species (Knight 1986).

Animal behavior focus: Frugivore preferences for native vs. non-native fruits matched for similarity

The small number of experiments that have examined frugivore preferences for native vs. non-native fruits that are similar in surface characteristics such as color and structure (e.g., both with red berries) have more often found preference for non-native than for native fruiting species (Table 1). Authors have suggested that frugivores use fine-scale differences to distinguish between similar food items. In two out of three aviary choice tests among color-matched pairs, European starlings and American robins preferred non-native over native fruits (LaFleur et al. 2007); the authors speculated that causal factors might include nutritional content and smaller relative seed mass (LaFleur et al. 2007). Captive American robins preferred similar native species to non-native *Viburnum opulus*, evidently due to low palatability of the introduced species (Jones and Wheelwright 1987). In a comparison of frugivory of native and invasive hawthorn (*Crataegus* spp.), bird attraction to larger pomes, greater fruit loads, and greater pulp to seed ratio were found to underlie a preference for the invasive species (Sallabanks 1993a). All of these characteristics imply that frugivores obtained a higher reward from each visit to the preferred plant than was available by visiting the less preferred. By contrast, frugivore-mediated fruit removal rates in North Carolina did not differ between invasive *Celastrus orbiculatus* and native *Ilex opaca*, which produce similarly colored and sized fruits, nor did fruit density per patch influence frugivory of *C. orbiculatus* (Greenberg et al. 2001). In this case, the authors suggested that normal bird flocking behavior was responsible for the lack of influence of per-patch fruit density on fruit removal as well as uneven fruit removal rates over the course of the season (Greenberg et al. 2001): birds likely moved from patch to patch and consumed resources opportunistically as they encountered them, rather than honing in on high-quality focal plants.

Frugivore preferences within existing suites of fleshy-fruited species

When combinations of native and invasive species in existing plant communities have been examined for frugivore preference, most studies have detected lack of preference or preference for native fruits (Table 1). No significant preference for either native or non-native fruits was observed when fruit removal by birds of two non-native and five native tree species co-occurring in Argentina was examined (Montaldo 2000). Birds consumed both native and non-native fruits at rates proportional to their availability, implying opportunistic consumption (Montaldo 2000). Opportunism has likewise been apparent in systems where non-native species offer fleshy fruits during a different season than the normal native fruiting season (White and Stiles 1992, Gosper 2004, Corlett 2005, Ferreras et al. 2008, Greenberg and Walter 2010, White and Vivian-Smith 2011); thus, non-native species benefit by supplying a resource that is otherwise rare or unavailable. On the other hand, distinct preference structure was detected in a suite of co-occurring

fleshy fruited plants in Maine, but no consistent factor underlying preference was detected: one non-native species and one native species experienced significant frugivore preference, while one non-native and one native species were less preferred (Drummond 2005). When offered paired choices between non-native *Adisia crenata* and a variety of native species, native birds in Florida almost unilaterally preferred native species, although the cause of such preferences were not elucidated (Meisenburg 2007). Preferences of native birds in a series of field and aviary experiments in Illinois varied by context, but under several conditions native *Phytolacca americana* was preferred above non-native *Eleagnus umbellata* and *Lonicera maackii* (Whelan and Willson 1994), leading the authors to suggest that making native fruits available to dispersers could enhance management of non-native species. In western Massachusetts, frugivorous birds utilized native fruits more than non-natives, and bird body condition was better in sites dominated by native species (Labbe 2011). By contrast, native birds in Pennsylvania achieved highest density and also elevated consumption of native fruits in areas of high invasive plant density (Gleditsch and Carlo 2011). Individual American robins displayed varying preference hierarchies when offered two non-native and one native fruit species that co-occurred in Wisconsin and varied in color and fruit type; bird body size appeared to influence choices more consistently than fruit characteristics (Jung 1992). The identity, origin, and native range of the frugivores themselves may also play a role. In diverse community of native and non-native fruits in New Zealand, endemic birds consumed far more native fruits than non-native fruits, while non-endemic and non-native birds acted more opportunistically and consumed both native and non-native fruits readily (Williams and Karl 1996). Notably, the sole preference study we found in which the disperser was an invertebrate showed results contrasting with the general trend in this category. Reward content relative to diaspore size was important for ant dispersal in Australia, where non-native ants preferentially dispersed small non-native seeds with large elaiosomes rather than larger native seeds (Rowles and O'Dowd 2009).

Meta-analysis: Frugivore preferences for native vs. non-native fruit

Because such a small number of studies have directly compared frugivore preferences for native vs. non-native fruits, a quantitative examination of combined study results has limited power. Therefore, although we conducted an exploratory meta-analysis to evaluate overall trends, we consider meta-analysis results preliminary and urge further study before general conclusions regarding frugivore preferences may be drawn.

Meta-analysis methods

For our meta-analysis, we used the response ratio to compare effect sizes between studies (Rosenberg et al. 2000). This metric is calculated as:

$$\ln R = \ln \frac{\bar{X}^E}{\bar{X}^C}$$

where $\bar{X}^E$ is the weighted mean of the proportion of non-native fruits consumed and $\bar{X}^C$ is the weighted mean of the proportion of native fruits consumed. Using this metric, a negative mean effect size with a 95% bias-corrected confidence interval excluding zero indicates that native fruits are consumed significantly more than non-native fruits. A positive mean effect size with a 95% bias-corrected confidence interval excluding zero indicates that non-native fruits are consumed significantly more than native fruits. We used a random-effects model and generated confidence intervals using 5000 data randomizations (Rosenberg et al. 2000). To examine the influence of matching external fruit characteristics on experimental results, we conducted a categorical analysis in addition to the overall meta-analysis. Although meta-analysis weights effect sizes by the sample sizes and variances of the component studies, several of the studies we utilized omitted variance information from their results. Because the overall sample size of studies available to us was so low, we preferred to include as many studies as possible in the meta-analysis and therefore conducted an unweighted meta-analysis (after Johnson and Curtis 2001), in which variances for all component studies were set equal to 1. All meta-analysis calculations were performed in MetaWin 2.0 (Rosenberg et al. 2000).

Meta-analysis results

The overall meta-analysis detected no significant difference in frugivore consumption of native vs. non-native fruits (mean effect size = -0.21, 95% bias-corrected confidence interval -0.35 to 0.07, n = 12 studies). However, categorical analysis detected differences between studies examining matched vs. unmatched fruits. For studies in which fruits were matched by external characteristics, there was no significant difference in frugivore preference between native and non-native fruits, but a trend toward preference for non-native fruits was visible (mean effect size = 0.37, 95% bias-corrected confidence interval -0.16 to 0.91, n = 4 studies). For studies in which no attempt was made to match fruits, frugivores demonstrated significant preference for native fruits (mean effect size = -0.31, 95% bias-corrected confidence interval -0.37 to -0.03, n = 8 studies). Again, the number of studies available for each category was small enough that these meta-analysis calculations had low power and results should be treated with caution.

Case study: Bird preferences among fleshy-fruited species in northern California

We conducted two aviary feeding preference experiments using wild-caught birds and fleshy-fruited plants in northern California. Our results illustrate the importance of fruit similarity in experimental conclusions.

Field-based foraging observations on fleshy fruits in California demonstrated higher visitation and fruit consumption rates for native *Heteromeles arbutifolia* than for co-occurring non-natives *Olea europaea*, *Ligustrum lucidum*, and *Triadica sebifera* (Aslan 2011). To determine whether quantitative preference hierarchies were consistent with these observed foraging rates, we conducted aviary-based feeding trials, offering fruits of the four focal plant species to wild-caught individuals of two native bird

species and one non-native bird species. In a separate study using a single native bird species, we examined preference hierarchies of birds offered native *H. arbutifolia* along with three non-native species selected for strong surface resemblance between their fruits and those of *H. arbutifolia*.

Case study methods

Preference hierarchy within an existing suite of fleshy-fruiting plants

The four non-native plants used in the first experiment are widely planted in the Sacramento Valley of California, co-occurring with the native species in many locations. *Olea europaea* L. (European olive, Oleaceae) produces racemes of large (ranging from 6–21 mm width), dark-purple drupes with high oil content and has become invasive in Australia (Spennemann and Allen 2000). *Ligustrum lucidum* W. T. Aiton (glossy privet, Oleaceae) invades natural areas in Australia and Argentina (Panetta 2000, Lichstein et al. 2004). Fruits are small (4–5 mm width) dark-purple berries produced in panicles with up to 3 million fruits per tree (Swarbrick et al. 1999). The plant's moisture requirements likely limit it to riparian areas in California. *Triadica sebifera* (L.) Small (Chinese tallow, Euphorbiaceae) produces round (7–8 mm width), white fruits in dehiscing capsules. Fruits consist of a seed with a hard coat surrounded by a waxy, lipid-rich aril. *Triadica sebifera* has become invasive in the southeastern United States (Bruce et al. 1997). In California, it is common in landscaping and spreads locally in a few riparian systems (Bower et al. 2009). These three non-native species were contrasted against the only simultaneously-fruiting and widespread native species: *H. arbutifolia* (toyon, Rosaceae). *Heteromeles arbutifolia* Lindl. (synonym *Photinia arbutifolia* Lindl.) produces red pomes (5–6 mm width) in panicles and is a largely upland, drought-adapted species. Nutritional analyses of the four plant species tested in this experiment show high similarity between *H. arbutifolia* and *L. lucidum*, which are both sugar-rich, and between *O. europaea* and *T. sebifera*, which are high in lipids (Supplementary table).

The bird species used in this experiment were selected to represent different functional guilds identified in field observations (Aslan 2011). American robins (*Turdus migratorius*) are native pulse feeders, feeding during winter in large flocks that move across the landscape and visit each fruiting stand in turn, removing most fruits there before moving on to a new feeding site. Hermit thrushes (*Catharus guttatus*) are native background feeders, present in each fruiting stand in low numbers throughout the season, with one or a few individuals exhibiting constant, low-level frugivory as long as fruits are present. European starlings (*Sturnus vulgaris*) are non-native pulse feeders that consumed non-native fruits far more than native fruits during field observations (Aslan 2011). Starlings were the top dispersers of *O. europaea* and *T. sebifera* in field observations; hermit thrushes were the top dispersers of *H. arbutifolia* and performed at least some dispersal for all four plant species; and robins were among the top four

dispersers for all four plant species (Aslan 2011). Robin and starling flocks were larger than those of other species observed during field observations (Aslan 2011), so the preferences of these two species have high potential to impact seed dispersal dynamics. All three focal bird species are more heavily frugivorous in winter in California than at other times of the year, when they become more omnivorous as more diverse food sources become available.

Ten robins were captured with mist nets in Butte County, CA, in December, 2007. Nineteen starlings were captured with walk-in traps in Marin County, CA, in November, 2008. Seven hermit thrushes were captured with mist nets in Butte and Yolo Counties, CA, in January, 2009. All birds were returned to open-air cages at the University of California, Davis. Cages measured 2.4 m tall, 1.5 m wide, and 3.8 m long. A single bird was housed in each cage and opaque green shade cloth was attached to walls between cages to prevent birds from observing and mimicking one another. Cages were roofed with metal sheeting to shelter birds from precipitation but were open at either end to allow natural sunlight and airflow/temperature. Birds were kept in cages for 10 days following capture to enable them to adapt to cage conditions. During this period, birds were provided *ad libitum* a maintenance diet with a banana/soy protein base (Denslow et al. 1987), supplemented with mealworms (10 per bird per day). Roudybush crumble maintenance diet (Roudybush, Inc., Woodland, CA) and moistened Eukanuba Small Bites Puppy Chow (Iams Co., Dayton, OH) were also made available to all birds, although these appeared to be consumed only rarely. Maintenance food was refreshed twice daily. Experimental treatments started on the 11th day of captivity; throughout the experimental period, the same maintenance diet was returned to the cages each day after experimental trials were completed (approximately 2 hours after sunrise) and remained available to birds for the remainder of the day. Birds were provided with water *ad libitum* at all times during captivity. Birds were weighed twice per week for the duration of the experiment to ensure that they were maintaining body weight; body weights decreased on average 10% during the first week of the experiment before stabilizing for the remainder of the captivity period.

For choice tests, experimental fruits were hung from weighted fishing line attached to cage ceilings. Fresh infructescences were collected from plants during the morning of each trial and were suspended from fishing line by looping the line around the infructescence stems. A separate line was used for each plant species so that the infructescences were presented to birds in a row across one end of the cage, separated from one another by approximately 30 cm. A long perch was hung in front of the row of fruits, allowing the bird easy access to all fruits. The fishing line allowed infructescences to bounce naturally as the bird foraged, mimicking branch movement in the wild. Whole infructescences were used so that the appearance, relative abundance, and arrangement of fruits reflected those encountered in the field. There was no attempt to artificially enhance similarity between plant species by controlling for fruit size or per-infructescence fruit abundance. Size differences between fruits are so great that any

attempt to equalize mass, for example, would require a given trial to utilize a very small number of *O. europaea* fruits relative to the number of *L. lucidum* fruits, skewing food item abundance dramatically. Whole infructescence use resulted in *L. lucidum* being the most numerous fruit offered, while *O. europaea* was usually offered in the greatest mass. Statistical analyses took into account initial availability of each fruit species per trial. At the end of each trial, fruits of all four species remained in all bird cages, demonstrating that quantities initially provided were sufficient to allow birds to make choices throughout the duration of each trial.

Choice trials were conducted as follows: Each phase of choice trials lasted six days. Just before daybreak on each day, one ripe (containing only fruits visibly as bright in color as any available on regional source trees) infructescence of each of the four study species was placed in each cage. Birds had fasted overnight. Infructescences were hung in random order from the fishing lines so that the arrangement differed from day to day. All birds were offered all fruits each day. All fruits were counted prior to their placement in the cages. Birds were allowed to forage freely for two hours. Birds showed evidence of hunger during this time, since most birds foraged, but not starvation (on some days, a minority of birds did not forage during the two-hour period). At the end of this period, all infructescences were removed and maintenance food replaced in cages. The final numbers of fruits per infructescence were counted to determine how many fruits had been removed. Cage floors were inspected and any whole fruits that had been dropped or had fallen from infructescences were collected so that actual numbers of fruits consumed could be calculated. Samples of fruits of each species were then weighed so that approximate masses of fruits available and consumed could be estimated. The same fruit species were offered on each of the six days, and these days were considered subsamples for statistical calculations. This minimized the effect of weather and other factors that may have caused variation in birds' daily feeding behavior.

During the second experimental phase, the fruit species most preferred by each bird species was withheld in order to determine preference hierarchy among remaining fruit species (to force some birds to choose between species they had previously ignored). Again, results from each day within this phase were considered subsamples for calculation of within-phase preference. Because robins and hermit thrushes preferred the native *H. arbutifolia* during phase 1, a third experimental phase included the native fruit once again in the experimental array so that birds had all four options. This was to ensure that preferences for the native in phase 1 were not due simply to familiarity with the native fruit, since it is more widespread in northern California than are the target non-natives, which are still clustered around urban and agricultural areas. Because birds had consumed non-native fruits during phase 2, when no natives were available, we hypothesized that neophobia or any similarly transient cause of preference would be purged by phase 2. Phase 3 thus elucidated the robustness of the initial preference for the native fruiting species, determining whether birds maintained that preference even after demonstrated familiarity with non-native fruits.

Preference hierarchy among plants selected for resemblance

In the second experiment, seven hermit thrushes (captured and maintained following the same methods and facilities described above) were offered fruits of four species selected for their resemblance to one another in the surface characteristics of fruit color, shape, and size: native *H. arbutifolia* and non-natives *Cotoneaster pannosus*, *Photinia x fraseri*, and *Pyracantha angustifolia*. All three of these non-native species are in the family Rosaceae and produce panicles of small red pomes. *Cotoneaster pannosus* is considered a potentially invasive species in California due to its invasiveness elsewhere and observed spreading in natural areas (Bossard et al. 2000). *Pyracantha angustifolia* is invasive in Argentina (Tecco et al. 2006) in environmental conditions similar to those found in parts of California. No instances of invasion by *Photinia x fraseri* in any environment have been recorded. Infructescences of these species were offered side by side for a single experimental phase of ten days, and fruit availability and consumption were tracked following the same protocol as described above for the first experiment.

Statistical analyses

Number of fruits consumed is more relevant to seed dispersal than is mass consumed since the number of fruits translates directly to the number of seeds that could be dispersed. For simplicity, therefore, figures and tables include only results by number. All statistical tests were performed for mass as well, but results did not differ qualitatively from results by number.

Treating the days within each experimental phase as subsamples, we calculated mean numbers available and consumed of each fruit species by each bird. We used these averages to calculate the selection index (w_i) of each fruit species by individual bird: $w_i = o_i/p_i$, where o_i = the proportion of species *i* in the diet, and p_i = the proportion of species *i* available in the environment (Krebs 1999). Selection index values exceeding 1.0 indicate preference for a food item since it has been consumed more than is proportional to its availability. We compared selection indices for each fruit species by bird species, separated by experimental phase, using standard least squares analysis of variance with individual bird as a blocking factor. To satisfy model assumptions, selection index values were square-root transformed prior to the performance of the ANOVA. Results were back-transformed for data presentation in figures. For each significant ANOVA model, a Tukey HSD means comparison was used to detect significant differences among fruit species. For all tests, significance was accepted at $p \leq 0.05$. Statistical analyses were performed in JMP 5.0.1 (SAS Institute, 2002).

Results of the case study

For the first experiment, analysis of variance revealed significant feeding preferences by selection index for all bird species in all experimental phases (Table 2, Figure 1). Robins preferred native *H. arbutifolia* to other test fruits when the native was available. When *H. arbutifolia* was withheld, they preferred *O. europaea* (Figure 1a). On average, starlings preferred *O. europaea* to other experimental fruit species. When *O. europaea* was withheld, starlings avoided *T. sebifera* but preferred *L. lucidum* and *H. arbutifolia* equally (Figure 1b). Hermit thrushes preferred *H. arbutifolia* to other fruits (both first and third experimental phases). When the native was withheld, they preferred *O. europaea* to other fruits with *L. lucidum* as a close second (Figure 1c). *Triadica sebifera* was consumed least by all birds during all phases (Figure 1).

During the second experiment, when experimental fruits were selected for their similarity, hermit thrush selection indices displayed little preference structure (Table 3). Analysis of variance results showed no overall significant difference in feeding preference among the four red-fruited species (Figure 2; a = 0.05), although raw numbers demonstrated greater consumption of all three non-native fruits than of the native *H. arbutifolia*.

Table 2. Results of analyses of variance comparing fruit species selection indices (w_i) separated by bird species and by experimental phase. Individual birds were treated as blocks for analysis. Data were square-root transformed to meet assumptions of homogeneity of variance.

Bird species	Experimental phase	Source	DF	F ratio	Prob > F
American robin (*Turdus migratorius*)	1	Fruit	3	26.82	<0.0001
		Bird (Block)	9	0.4035	0.9222
	2	Fruit	2	13.68	0.0002
		Bird (Block)	9	0.6943	0.7058
	3	Fruit	3	55.07	<0.0001
		Bird (Block)	9	0.6974	0.7055
European starling (*Sturnus vulgaris*)	1	Fruit	3	13.68	<0.0001
		Bird (Block)	18	0.4404	0.9711
	2	Fruit	2	7.95	0.0014
		Bird (Block)	18	0.6810	0.8064
Hermit thrush (*Catharus guttatus*)	1	Fruit	3	33.82	<0.0001
		Bird (Block)	6	0.6470	0.6921
	2	Fruit	2	4.35	0.0380
		Bird (Block)	6	0.4374	0.8403
	3	Fruit	3	9.97	0.0004
		Bird (Block)	6	0.0911	0.9965
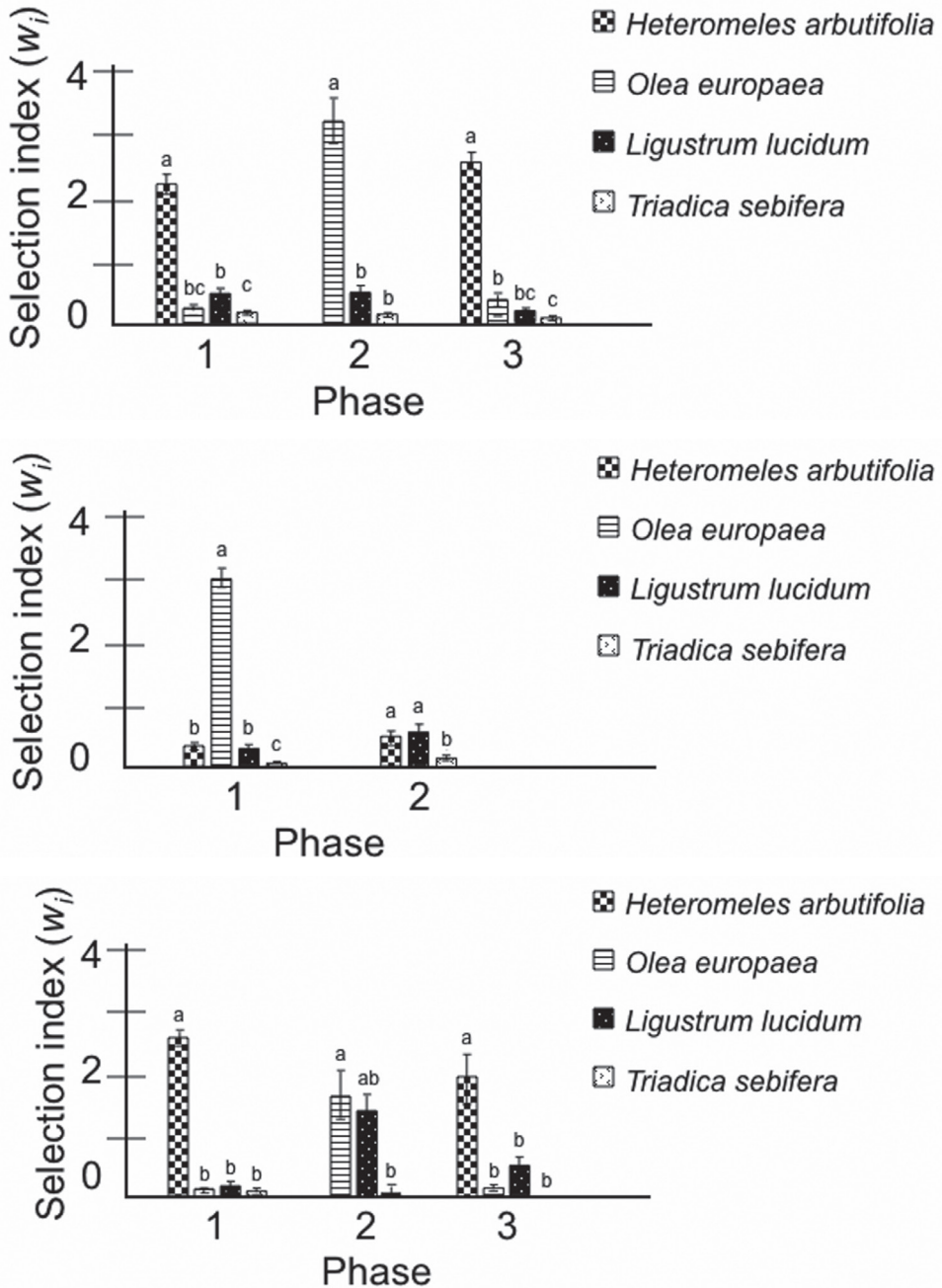
Figure 1. Mean (± SE) selection indices (w_i) by bird species and by experimental phase. Selection index values >1.0 indicate a preferred food item (consumed at a rate exceeding its availability). Analyses of variance with individual birds designated as blocks compared preferences within each experimental phase. Means within each ANOVA were compared using Tukey HSD means separation. Within each experimental phase, bars not designated by the same letter are significantly different at a = 0.05. **a** American robins (*Turdus migratorius*) **b** European starlings (*Sturnus vulgaris*) **c** Hermit thrushes (*Catharus guttatus*)

Table 3. Selection indices (w_i) for similarity experiment using red fruit and testing preferences of hermit thrushes (*Catharus guttatus*). Selection index values greater than 1.0 indicate preference by hermit thrush individuals for a food item, and these values are underlined. Values are presented for number of fruits as selection indices ± SE.

Bird	*Pyracantha angustifolia*	*Cotoneaster pannosus*	*Photinia x fraseri*	*Heteromeles arbutifolia*
A	0.12 ± 0.21	0.36 ± 0.31	<u>2.51</u> ± 0.37	0.50 ± 0.32
B	0.26 ± 0.32	<u>1.30</u> ± 0.57	<u>1.32</u> ± 0.44	0.87 ± 0.48
C	<u>1.94</u> ± 0.70	0.98 ± 0.54	0.47 ± 0.36	0.82 ± 0.49
D	<u>1.12</u> ± 1.23	0.97 ± 1.06	0.80 ± 0.88	<u>1.21</u> ± 1.33
E	<u>2.95</u> ± 0.73	0.21 ± 0.26	0.96 ± 0.41	0.26 ± 0.29
F	0.50 ± 0.36	0.40 ± 0.28	<u>2.33</u> ± 0.32	0.36 ± 0.23
G	0.40 ± 0.39	0.93 ± 0.52	<u>1.60</u> ± 0.40	0.66 ± 0.43
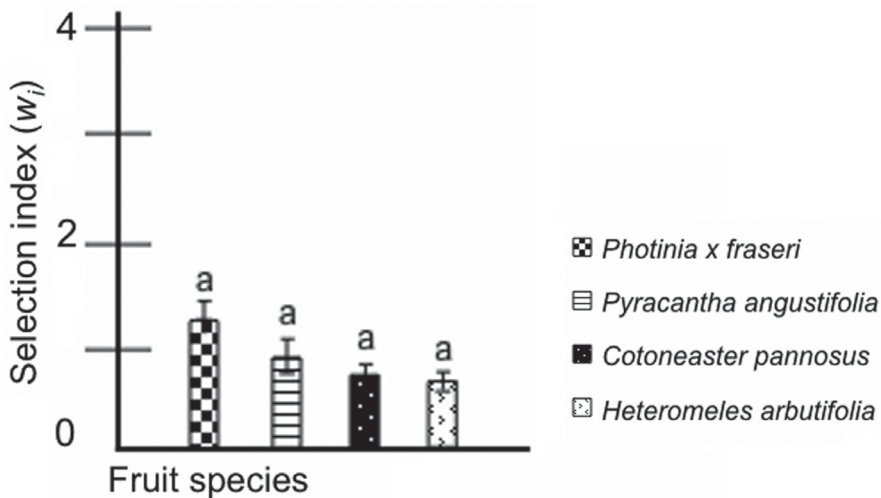
Figure 2. Hermit thrush (*Catharus guttatus*) fruit similarity experiment selection indices by fruit species. Mean selection indices were compared using analysis of variance, with individual bird as block. Means within each ANOVA were compared using Tukey HSD means separation. Within each experimental phase, bars not designated by the same letter are significantly different at a = 0.05.

Discussion

If native frugivores prefer introduced fruiting species in a given region, seed dispersal services are likely to be monopolized to some degree by the non-native plant species and withheld from native plants. Although the number of studies that have explored such

dispersal competition is quite low, our review and meta-analysis of their results and our case study experiments indicate that native fruit characteristics may play an important role in determining frugivore preference. When frugivore preference is evaluated in the context of the full existing suite of fleshy-fruited plants, with no attempt to artificially enhance similarity between species, frugivores tend to prefer native fruits. However, when non-natives that are similar to natives in surface appearance have been examined, frugivores have shown an inclination, often slight, to prefer the non-native fruits. In published literature, preference for non-natives appeared to result from larger crop sizes, higher per-fruit energy content, or larger fruits relative to seed mass, implying that such species are preferred because the reward is likely greater for a given frugivore visit. Thus, frugivores in these studies seem to demonstrate general attraction to certain characteristics typical of native fruits (such as color or shape), and it is within sets of species sharing these characteristics that more subtle preferences favoring non-native species appear.

In our case study experiments, for example, both native bird species preferred the native red berry even above *Ligustrum lucidum* with its very large crop sizes of dark purple berries, although the two are extremely similar nutritionally. When the native fruit was contrasted against non-native, red-berried species offered to hermit thrushes, however, this strong preference for the native fruit disappeared. Birds that had displayed highly significant preference for native fruits displayed no significant preference structure when similar fruits were introduced. The non-native bird species, on the other hand, showed no preference at any time for the native species. The native bird fauna appears to maintain a robust preference for red-berried species, which could be the result of loose coevolution between the birds and fruits in the area: since the most available native fruit during the winter season is red, a preference for that color among native birds is unsurprising. When non-native species producing red berries are introduced to this system, they are likely preadapted to ready winter seed dispersal. As long as they produce larger or more accessible crops, they may draw dispersers away from the native species. By contrast, fruits of different color or structure from the native appear less preferred, likely because they lack such preadaptation. Under this scenario, native fruit characteristics appear to play a key role in determining whether native and non-native fruits will compete for dispersers. Introduced species sharing these characteristics (red berries) are most likely to exert a competitive impact. An important consideration is that bird adaptation to prefer a given native fruit may arise because that native fruit is a particularly suitable food source, for example contributing to higher bird fitness by offering high nutritional value. Decline in such fruit species through a competitive effect may therefore impact native bird populations.

Non-native frugivores may also affect seed dispersal. Such species have enhanced the dispersal of native species in some systems (Foster and Robinson 2007), while in others they facilitate invasions by non-native species (Mandon-Dalger et al. 2004). In our case study experiments, European starlings preferred non-native *Olea europaea* fruits, and they were dominant visitors to all three target non-native species in field observations (Aslan 2011). The preference hierarchy and foraging pattern displayed by starlings differed considerably from those observed in native bird species. Since intro-

duced birds and native plants do not share an evolutionary history, it is unsurprising that they lack the tight linkage imposed by bird feeding preferences. It appears logical that the pattern we observed would also be found in other systems, although the preferences of non-native frugivores have been explored in only a handful of studies (e.g., Williams 2006, LaFleur et al. 2007, Kawakami et al. 2009). We thus qualify that the importance of native fruit characteristics, as discussed above, seems likely to diminish if a substantial portion of the local frugivore fauna is introduced.

Conclusion

The review, meta-analysis, and aviary experiments examined here suggest that frugivores are most likely to favor non-native fruits if they resemble preferred native fruits, at least on the surface. In several instances, frugivores have shown preference for non-native species that are selected to resemble native species in fruit color or type. When such introduced species offer a larger number of fruits per plant or relatively higher quantity of digestible material per fruit, they appear to attract more frugivory than the natives and thus have the potential to display a competitive edge over native fleshy fruits. When non-native species differ from natives in superficial characteristics such as fruit color or type, studies show a tendency for frugivores to prefer native species or at least to feed opportunistically. This pattern implies that non-native fruits are most likely to encounter preferential frugivory and thus to compete for dispersers with native fruits if they resemble those native fruits and offer enhanced feeding efficiency. When these conditions are met, competition for dispersers and eventual decline in the dispersal of native species may occur following fleshy-fruiting plant introductions.

If it is indeed widespread across geographies, such competition has implications both before and after plant introductions. When new plants are considered for a region, as horticultural, agricultural, or landscaping introductions, they may be most likely to encounter frequent dispersal and to exert competitive impact if they resemble preferred native plants and overlap with natives in fruiting phenology. Along with other known invasive impacts of such species, dispersal competition should be considered a potential additional impact of their introduction, and should be taken into account. Control of such species in favor of the native should be considered.

To date, the number of studies directly addressing seed disperser preference for native vs. non-native fruits is very low, and study designs differ considerably. A greater number of such studies will be necessary in order to evaluate with confidence how widespread these patterns may be. In addition, we recommend use of standardized methodologies (such as those described in Manly et al. 2002) that include comparisons of both similar and dissimilar fruits, in order to account for the role of native fruit characteristics in preference development. To our knowledge, no studies of exotic vs. native preference among two important groups of tropical dispersal agents, bats and primates, nor of frugivorous predators (D'hondt et al. 2011) have so far been conducted. Expansion of

the taxonomic scope of the literature to include these and other groups, including further exploration of invertebrate dispersers, would be beneficial. Once the sample size of available studies has grown, a more robust meta-analysis may be useful to pinpoint more precisely the conditions under which seed dispersers favor non-native fruits.

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Supplementary table. Nutrient content of the four focal fruit species. Values are for fruit pulp, the fruit portion assimilated in most cases by frugivorous birds, which usually defecate or regurgitate seeds. Nutrient content analyses were conducted by a commercial food analysis company (National Food Laboratories, Inc., Livermore, CA).

Nutritional component	*Heteromeles arbutifolia*	*Olea europaea*	*Ligustrum lucidum*	*Triadica sebifera*
Fructose (%)	0.62	0.11	2.77	<0.25
Glucose (%)	5.06	1.06	5.80	<0.25
Lactose (%)	<0.25	<0.25	<0.25	<0.25
Maltose (%)	<0.25	<0.25	<0.25	<0.25
Sucrose (%)	<0.25	<0.25	0.63	2.27
Total Sugars (%)	5.88	1.67	9.71	2.27
Ash (%)	1.14	2.28	1.84	2.33
Calories (cal/100g)	134.07	346.21	95.07	1038.46
Carbohydrates (%)	33.28	22.04	25.75	3.16
Moisture (%)	64.91	45.78	72.24	28.01
Protein (%)	0.67	2.18	0.17	<0.25
Total Fat (%)	<0.25	27.71	<0.25	66.5

RESEARCH ARTICLE

Potential distribution range of invasive plant species in Spain

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Abstract

Success of invasive species has been frequently estimated as the present distribution range size in the introduced region. However, the present distribution range is only a picture of the invasion for a given time step and do not inform on the potential distribution range of the species. Based on niche-based models we used climatic, geographic and landscape information on the present distribution range for 78 major plant invaders in Spain to estimate and map their potential distribution range. We found a positive relationship between present and potential distribution of species. Most of the species have not yet occupied half of their potential distribution range. *Sorghum halepense* and *Amaranthus retroflexus* have the widest potential distribution range. *Sorghum halepense* and *Robinia pseudoacacia* have the highest relative occupancy (i.e. proportion of potential distribution range currently occupied). Species with a larger minimum residence time have, on average, higher relative occupancy. Our study warns managers that it might be only a matter of time that currently localized invasive species reach their potential area of distribution.

Keywords

Introduction

Invasive plant species are defined as alien species that sustain self-replacing populations without direct human intervention. They produce offspring, often in very large numbers, at considerable distances from the parent plants, and thus have the potential

to spread over a large area (Pyšek et al. 2004). Yet, the spread rate of invasive species differs considerably. The distribution of invasive species is not static. There might be large differences between the present and potential distribution ranges of invasive species (Higgins et al. 1996, Sakai et al. 2001). From a management point of view, it is extremely important to identify areas not yet invaded but where early warning detection and control programs are critical to implement.

Up to now, most efforts to evaluate the success of invasive species at the regional scale have been traditionally measured as the present distribution range in the region of introduction (Mack et al. 2006). However, the present geographical range size shows only a picture of the degree of invasion for a given time step, but it does not inform about the dynamics of invasion and the potential invasion range in the near future. Recent studies have developed niche-based models to assess the suitability of a region for a given invasive species and its potential to spread throughout (Petterson 2003, Rouget et al. 2004, Guisan and Thuiller 2005, Thuiller et al. 2005). These models are mainly based on the climate matching approach (Curnutt 2000, Pauchard et al. 2004, Watt et al. 2010, Kriticos et al. 2011). However, even at the regional scale, other factors determine the distribution of species including biotic interactions, evolutionary change and dispersal ability (Pearson and Dawson 2003, Ibáñez et al. 2006). For invasive species, direct and indirect human assisted dispersal is a primary determinant of species distribution. This is the reason why recent estimations of the distribution area of invasive species incorporate geographical and landscape variables related to human activities and disturbances (Pino et al. 2005, Thuiller et al. 2006, Chytrý et al. 2008, Gassó et al. 2009).

Moreover, historical factors determining differences in propagule pressure such as the minimum residence time (i.e. time since first record) also influence the range size of invaders (Hamilton et al. 2005, Gassó et al. 2009, Ahern et al. 2010). Due to lag times, the longer the species is present in the region, the more propagules are spread and the probability of founding new populations increases (Crooks 2005, Lockwood et al. 2005). Therefore, the relationship between range size and residence time should be considered. If there is a positive relationship between the proportion of the potential distribution range currently occupied and the minimum residence time, we can consider that it is only a matter of time for a localised invasive species to become widespread.

Here we calculated and mapped the potential distribution ranges of the main invasive plant species in Spain using climatic, geographic and land use variables. This research is planned to assist environmental managers to estimate the risk of present alien invasive species to expand into non-invaded areas. Mapping the potential distribution of species in areas were they are still not occurring is of high priority for the regional administrations to fulfil the Spanish List and Catalogue of Invasive Exotic Species Act 1628/2011 (http://www.boe.es/boe/dias/2011/12/12/pdfs/BOE-A-2011-19398.pdf). Our main questions are: (i) To what extent is the potential distribution range related to the present distribution range? (ii) What is the mean proportion of potential distribution range currently occupied (i.e. relative occupancy)? (iii) Does relative occupancy depend on the minimum residence time of the species?

Materials and methods

Species distribution

Distribution data and minimum residence time (i.e. earliest date on which a given species was recorded in Spain) were compiled from the Atlas of Invasive Plant Species in Spain (Sanz-Elorza et al. 2004). This atlas contains spatially explicit presence records for over 100 invasive alien plant species at a resolution of 10×10 km UTM (Universal Transverse Mercator) grid. The atlas was generated using several information sources: herbarium records, publications and field surveys. From the initial database, we only calculated the potential distribution range for neophytes (i.e. established aliens introduced after 1500) recorded in more than 10 UTMs. We did not include archaeophytes because the minimum residence time is unknown. We also excluded UTM cells with a land proportion of less than 60% to avoid large differences of land proportion per UTM cell. Overall, our analysis is based on 2401 UTM cells and 78 invasive species (Appendix I).

Environmental data

Environmental data were obtained from different data sources that were originally at different resolutions, but we aggregated each one of them to a 10x10 km UTM grid cell scale by averaging. All the GIS procedures involving the set up of the environmental variables were performed using MiraMon (Pons 2000); mapping was performed with ArcView (ESRI 1992-2006).

The selection of environmental variables was based on preliminary results on variables strongly related to invasive plant species richness in Spain (Gassó et al. 2009). These included 3 climatic variables (minimum temperature in winter, annual temperature range, and summer rainfall), a reduction of 10 landscape variables to 5 using a principal component analysis (PCA), and keeping the first five orthogonal axes (cumulated explained variance = 80%) and one geographic variable (distance to the coastline) (Table 1).

In Spain, distance to coastline encompasses a complex gradient. Coastal areas concentrate the tourism, trading and transport centres, as most of the first records of alien species (Sanz-Elorza et al. 2004, Gassó et al. 2009). Moreover, due to the continental effect and the natural topography of Spain (i.e. high plateau in the centre), there is a climatic gradient from mild climatic, lowland conditions in the coast to contrasted, mountain climate inland. In consequence, distance to the coast is strongly and negatively correlated with annual temperature range (i.e. difference between maximum temperature in July and minimum temperature in January). In order to keep distance to coastline into the model despite its association to annual temperature range, we adjusted distance to coastline by fitting a univariate non-linear regression (generalised additive model with 4-degrees of freedom) with annual temperature range as the pre-

Table 1. Initial set of environmental predictors to estimate potential distribution ranges of 78 invasive plant species in Spain. Landscape variables were reduced from 10 to 5 using a principal component analysis (PCA) and keeping the first five orthogonal axes (cumulated explained variance = 80%). Distance to the coastline and 3 climatic variables were also selected. For distance to the coastline we used the residuals from the regression with annual temperature range as predictor variable. For summer rainfall, we used the residuals from multiple regressions with annual temperature range and minimum winter temperature as predictor variables (for more details see Thuiller et al. 2006).

Variables	Data source	Transformation
Landscape		
Built-up areas (%)		PCA
Agricultural areas (%)		PCA
Forests (%)		PCA
Scrub and herbaceous associations (%)		PCA
Open spaces (%)	CORINE Land Cover Map of Spain (http://www.fomento.es)	PCA
Wetlands (%)		PCA
Water bodies (%)		PCA
Land cover diversity (Shannon Index)		PCA
Roads length (m)	Official server of the Spanish	PCA
Railway length (m)	Ministry (http://www.cnig.es)	PCA
Geography		
Mean distance to the coastline (m)	Digital Elevations Model (http://www.opengis.uab.es)	Residuals
Climate		
Annual temperature range (max July - min January)	Digital Climatic Atlas of Spain (http://opengis.uab.es/wms/iberia/index.htm)	Non transformed
Minimum winter temperature (°C)		Non transformed
Summer rainfall (mm)		Residuals

dictor variable. We then used the residuals of the univariate regression as a predictor into the model. We followed the same strategy for summer rainfall which was correlated with minimum winter temperature and annual temperature range as predictor variables (for more details on the approach, see Thuiller et al. 2006).

Estimation of potential distribution ranges

Because a precise native distribution was not known for most of the species selected, we estimated the potential range of each species using climatic, geographic and landscape information from their present distribution in Spain (see Wilson et al. 2007 for more details on the approach).

Considering that our goal was to estimate and map the potential distribution of 78 invasive species, it was impossible to find good climatic data from the native range for

all species. However, notice that we did not solely base our analysis on climatic data but also on geographic and landscape data. These variables account for habitat invasibility and propagule pressure influencing on the degree of invasion. Therefore, even if possibly our models might be climatically conservative they included other relevant landscape variables known to influence the degree of invasion (Vilà and Ibáñez 2011). Considering that the grain of the analysis are 10×10 km UTM grids, these maps can be used as tools for risk analysis for the different Spanish administrative regions (e.g. early warning maps for species that have still not invaded a particular administrative region).

The potential distribution range of each species was modelled as a function of the 9 selected environmental variables. All the modelling process was performed using the BIOMOD application implemented under R software. We calibrated 4 models usually described as the most powerful approaches available (Elith et al. 2006, Prasad et al. 2006): generalised linear models (GLM) using a stepwise regression with AIC criteria, generalised additive models (GAM) with four degrees of smoothing using a stepwise regression with AIC criteria, Random Forest (RF) with 2000 trees, and Generalised Boosting Models (GBM) with 3000 trees and an interaction depth of 2. Models were calibrated using 70% of the initial data sets and evaluated on the remaining 30% using the Relative Operating Characteristic (ROC) curve procedure.

To avoid the usual trouble of selecting a particular model, we performed a weighted averaging procedure across our four models as recommended by Marmion et al. (2009). For each species, the four models were ranked according to the area under the ROC curve values (AUC), and only the best three predictions (i.e. from the best three models) were conserved and were awarded 3, 2 or 1 point(s) respectively and then standardized to produce a vector of weights whose elements sum to unity. Final projections consisted in the weighted average of these three simulations. Then, for each species, we transformed the averaged predictions into presence–absence using a threshold maximizing the percentage of presence and absence correctly predicted (Pearce and Ferrier 2000). For these averaged predictions, the accuracy of the simulations was assessed using the area under the ROC curve (AUC). We used the following conservative rough guide for the AUC: AUC<0.8, bad model; 0.8<AUC<0.9, good model and AUC>0.9, very good model.

Statistical analyses

We analysed the relative occupancy as a function of minimum residence time. Relative occupancy was calculated as the proportion of potential distribution range currently occupied by each species. Relative occupancy was expressed as a binary variable with the first column containing the number of UTM cells currently occupied and the second column with the number of potentially suitable UTM cells not yet occupied. Minimum residence time was log transformed before analysis to meet the assumptions of parametric analysis.

Invasive species are a non-random subset of all species introduced (Blackburn and Duncan 2001). Furthermore, species are linked by phylogeny (Harvey and Pagel 1991). Therefore, using species as independent data points may inflate the degrees of freedom and increase the Type-I error. We used Generalized Linear Mixed Models (GLMM) to deal with the phylogenetic effects by incorporating taxonomic categories as nested random factors (Family/Genus). Several sophisticated procedures are available to implement phylogenetic structure in the model, but, in our case, there was not any robust phylogeny available covering all studied species.

Analyses were conducted in the open source R software version 2.5.1 (R Development Core Team 2005). We modelled relative occupancy with a binomial distribution of errors using the glmmPQL of the MASS library on the R statistical package (Venables and Ripley 2002, R Development Core Team 2006).

Results

We are confident that our models to estimate the potential distribution range were very good because for most species AUC>0.9 (Appendix I). As expected, there was a positive relationship between present distribution ranges (CDR) and potential distribution ranges (PDR). However, present distribution ranges only explained half of the variance of the potential distribution ranges (PDR = 309.3 + 0.89CDR, R^2 = 0.53, $F_{(1, 76)}$ = 85.44, p < 0.01). There was a set of species, especially those that currently occupy less than 200 UTM that, according to our models, would have the potential to spread through larger areas than that expected by the linear relationship (Fig. 1).

The species with the widest potential distribution ranges were *Sorghum halepense,* considered as one of the top weeds in the world (Holm et al. 1977) and *Amaranthus retroflexus*, also a worldwide invader, both of them invading many different habitat-types (Sanz-Elorza et al. 2004). These two species were introduced more than 100 years ago and exhibit wide present distribution ranges, being spread already in more than half of their potential distribution range.

The mean (±SE) relative occupancy of species was 0.28 ± 0.02; with values ranging from 0.05 to 0.73. Most of the species have not yet occupied half of their potential geographic ranges (Fig. 2). The two species with the lowest relative occupancy were the shrub *Senecio inaequidens* (0.28) and the herb *Tradescantia flumminensis* (0.23), and the two species with the highest relative occupancy were the deciduous tree *Robinia pseudoacacia* (0.73) and the grass *Sorghum halepense* (0.72) (Fig. 3).

Having accounted for the potential phylogenetic effects, the glmmPQL showed that minimum residence time explained a significant portion of variance in relative occupancy (t = 3.9, p<0.0001). Species introduced earlier had, on average, occupied a higher proportion of their potential distribution range (Fig. 4). However, it is interesting to note that the relationship is not linear, with some species introduced a long time ago (i.e. 400–450 years) having still a very restricted distribution with respect to their modelled potential distribution range.
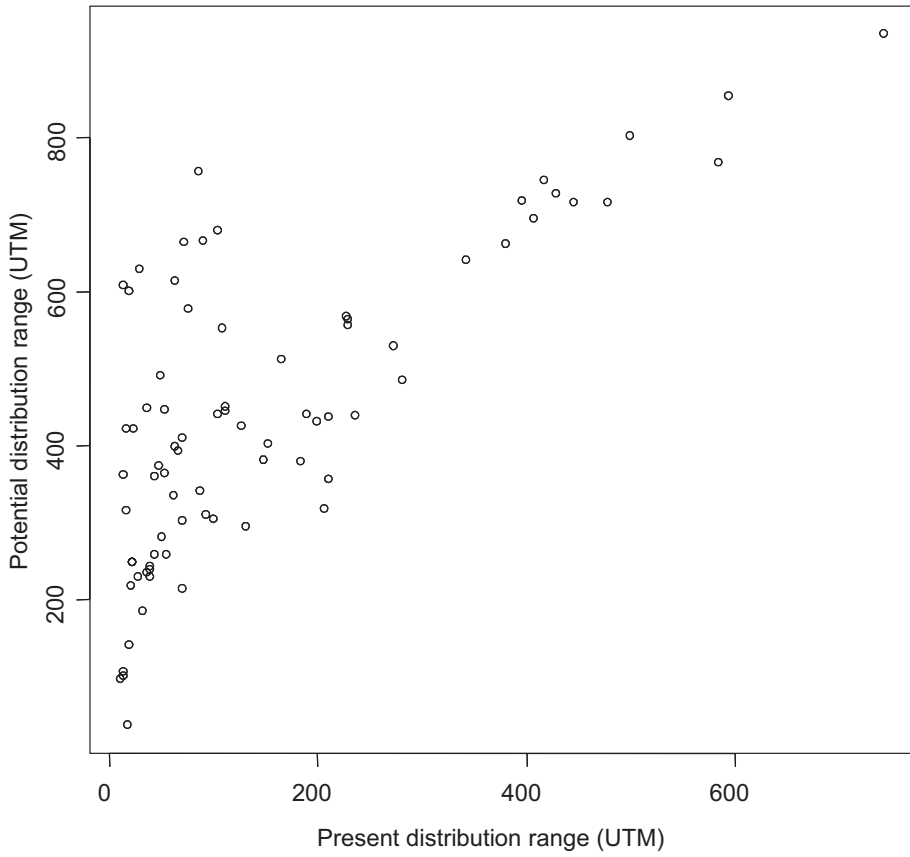
Figure 1. Relationship between present (CDR) and potential (PDR) distribution ranges for 78 invasive plant species in Spain. PDR = 309.3 + 0.89CDR, R^2 = 0.53, $F_{(1, 76)}$ = 85.44, p < 0.01.
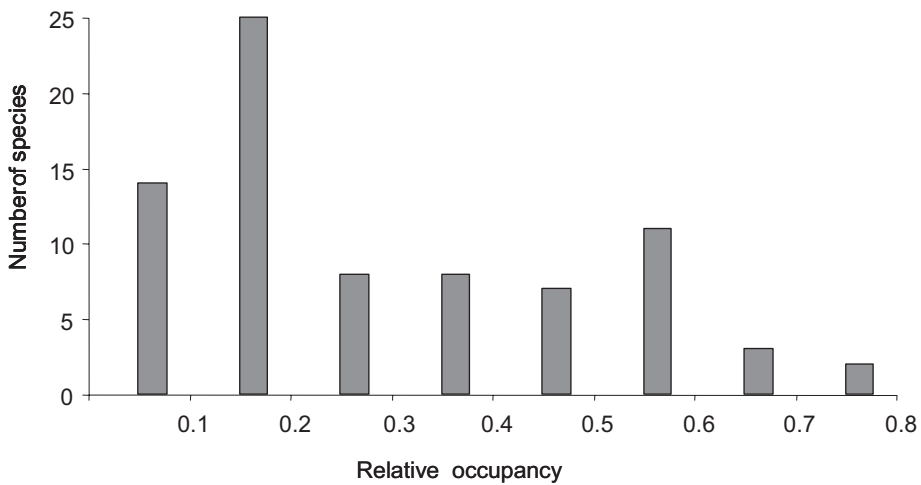
Figure 2. Frequency distribution of relative occupancy (i.e. proportion of the potential distribution range currently occupied) by invasive plant species in Spain (N = 78).
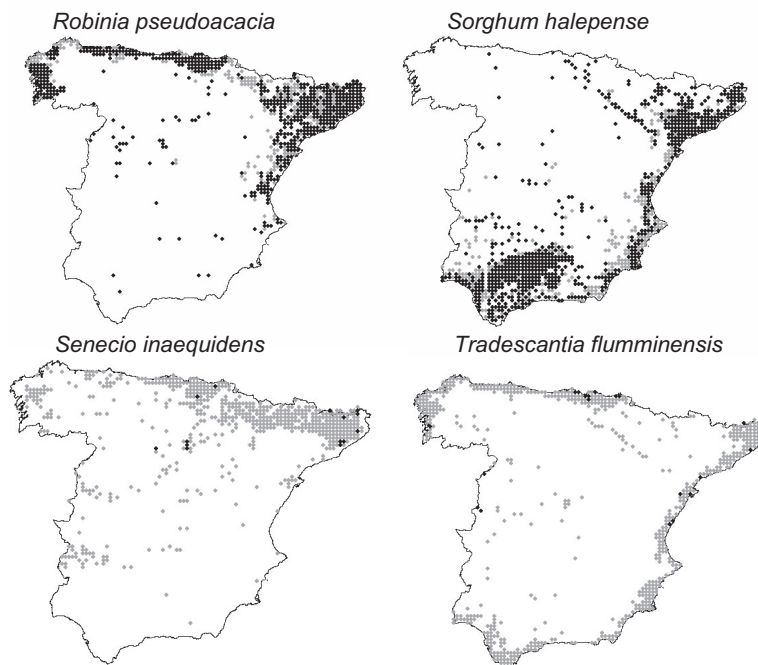
Figure 3. Maps of present distribution range (black) over potential distribution range (grey) of four invasive plant species in Spain. The two species on top are the ones with the highest relative occupancy (i.e. proportion of the potential distribution range currently occupied) and the ones at the bottom are those with the lowest. Maps for the remaining analysed 74 invasive species are available in Appendix II.
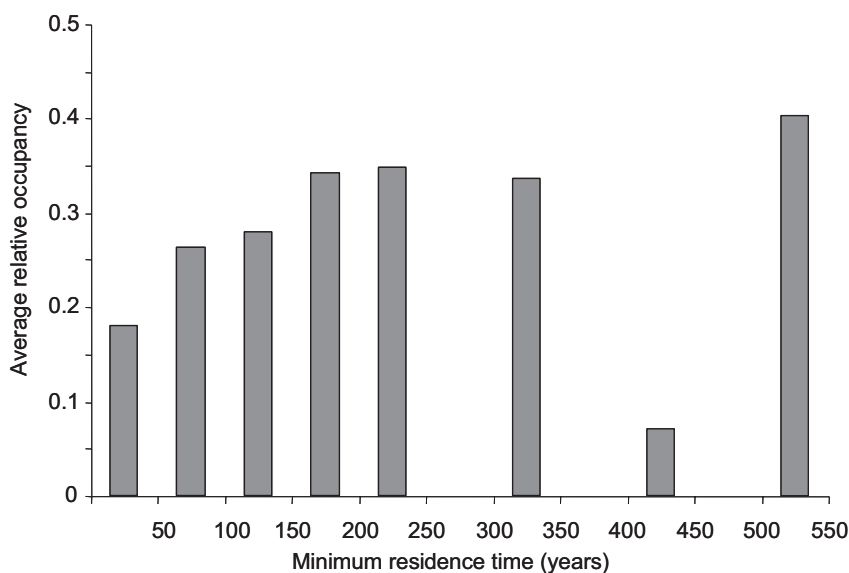
Figure 4. Average relative occupancy (i.e. proportion of the potential distribution range currently occupied) for minimum residence time classes of invader plant species in Spain (N = 78).

Discussion

We found large differences among species in their potential distribution range in Spain. However, in general, invasive species have not yet reached half of their potential distribution ranges. On average, it takes around 150 years for a neophyte to reach its maximum distribution range in an European country (Gassó et al. 2010) and many invasive species in Spain have been introduced less than a century ago (Sanz-Elorza et al. 2004).

Our calculations of potential distribution ranges for the 78 invasive species are based on climatic conditions in the introduced range in Spain and not in the native range. Theoretically, modelling the potential distribution range of an alien species should be based on climate matching envelopes build with information from the native range where the species is at equilibrium (Jiménez-Valverde et al. 2011). It is possible that recently arrived species in Spain have not yet expanded to available localities of suitable climates. However, climatic information from the native range was not available for most species. Moreover, models build with climatic conditions in the native range assume that the same interactions between biotic factors and climatic factors that limit the range size in the native range operate in the introduced range (Pearson and Dawson 2003). This assumption might not be correct as plant fitness, population performance and distribution range of invasive species are usually improved in the introduced than in the native range (Hierro et al. 2005). It is clear that the interactions between biotic factors and abiotic factors in the native range are different than in the introduced range (Ibáñez et al. 2006, Wilson et al. 2007). Even if our estimations of the potential distributional ranges are probably conservative, we are confident that by including geographic and landscape variables in our models, the predictions are more accurate than by only including climatic variables (Ibáñez et al. 2009).

Results confirmed that relative occupancy was dependent on minimum residence time (Hamilton et al. 2005, Williamson et al. 2009, Ahern et al. 2010). In general, the longer an invasive species in a region, the more it extends into its potential range because it has had more opportunities to be introduced several times at various locations and more time to disperse naturally. In a previous work with a larger subset of species from the same data set, a relationship between present distribution range and minimum residence time was also found (Gassó et al. 2009). However, this association was not significant for species introduced during the last 100 years. Thuiller et al. (2006) also found that minimum residence time did not explain the distribution patterns of invaders in South Africa less than a century of residence. As previously mentioned, species distribution models assume that organisms are at equilibrium with their environment. Nevertheless, this might not be the case for recently introduced species (Václavík and Meentemeyer 2012). These species are listed as invasive in Spain due to their fast population growth at the local scale even if their regional spread might still be limited. The accuracy of potential distribution models for species at early invasion stages and with short minimum residence times is usually lower than for species from late invasion stages (Václavík and Meentemeyer 2012).

Similarly, the association between relative occupancy and minimum residence time is weak for species introduced many centuries ago (Williamson et al. 2009) because there is high uncertainly with old first records. Indeed, in Spain, some species introduced a long time ago have not yet occupied their entire potential suitable habitat. For example, *Sophora japonica* was introduced 304 years ago, but it currently occupies only 11.1% of its potential distribution range, demonstrating a very low spread rate. The low spread of this species could be related to the history of its use. It was first introduced in the country in the 18th century but it was not used commonly as an ornamental species until the 20th century (Sanz-Elorza et al. 2004). Besides minimum residence time, other historical factors such as the intensity and frequency of introduction determine propagule pressure and hence invasion success (Lockwood et al. 2005). For example, market availability (i.e. sold in many nurseries) and frequency (i.e. sold very often) are significant determinants of invasion by traded ornamental plant species (Dehnen-Schmutz et al. 2007). We can therefore suspect that in some species introduced several centuries ago there might be a substantial time lag between the date of first record and spread due to differences in historical propagule pressure (Crooks et al. 2005).

Besides propagule pressure, differences in the potential distribution range might be also explained by differences in their niche breadth (Thuiller et al. 2005) and the availability of suitable habitats for establishment. The potential distribution ranges calculated here are mainly based on abiotic factors defining a fundamental niche *sensu* Hutchinson and Deevey (1949), while species traits (e.g. reproduction or dispersal), local biotic interactions (e.g. competition, natural enemies, and mutualistic relationships), and geographical barriers for dispersal also influence alien species establishment and spread (Rejmánek et al. 2005, Ibáñez et al. 2006, Pyšek and Richardson 2006).

Our study has been possible because there was reliable spatially explicit data on the present distribution of invasive species (Sanz-Elorza et al. 2004). This empirical information, which has been a compilation of the effort by many naturalists and botanists, has been complemented by modelling approaches to estimate the potential distribution area of the species. More than half of the main invasive species in Spain have not reached their potential area of distribution. However, many species would be able to reach this area in the near future because many species are ornamental and dispersal is favoured by humans (Aikio et al. 2010). We believe that the potential distribution maps of these species are a crucial early warning tool to guide control and eradication plans even if the potential distribution for recent introduced invasive species is possibly underestimated.

Acknowledgements

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Appendix I

Minimum residence time (MRT; years), present distribution ranges (CDR; number of UTM 10x10 km), potential distribution ranges (PDR; number of UTM 10×10 km) and relative occupancy (i.e. proportion of the potential distribution range currently occupied) for 78 invasive plant species in Spain. PDR were calculated according to an averaged model of 4 potential distribution models for each species. The area under the ROC curve (AUC) of the averaged model is shown on the table.

Family	Species	MRT	CDR	PDR	OCCUPANCY	AUC
Malvaceae	*Abutilon theophrasti*	74	94	680	0.14	0.92
Fabaceae	*Acacia cyanophylla*	204	20	217	0.09	0.98
Fabaceae	*Acacia dealbata*	204	204	356	0.57	0.99
Fabaceae	*Acacia melanoxylon*	204	71	214	0.33	1.00
Aceraceae	*Acer negundo*	204	61	393	0.16	0.95
Asteraceae	*Achillea filipendulita*	22	18	37	0.49	1.00
Agavaceae	*Agave americana*	504	217	557	0.39	0.97
Simaroubaceae	*Ailanthus altísima*	186	210	563	0.37	0.96
Amaranthaceae	*Amaranthus albus*	143	408	716	0.57	0.95
Amaranthaceae	*Amaranthus blitoides*	94	445	715	0.62	0.96
Amaranthaceae	*Amaranthus hybridus*	124	368	718	0.51	0.94
Amaranthaceae	*Amaranthus muricatus*	96	189	432	0.44	0.97
Amaranthaceae	*Amaranthus powellii*	21	83	666	0.12	0.93
Amaranthaceae	*Amaranthus retroflexus*	104	551	854	0.65	0.94
Amaranthaceae	*Amaranthus viridis*	106	100	444	0.23	0.95
Asclepiadaceae	*Araujia sericifera*	28	90	311	0.29	0.98
Asteraceae	*Arctotheca calendula*	88	23	421	0.05	0.97
Asteraceae	*Artemisia verlotiorum*	91	158	512	0.31	0.97
Asteraceae	*Aster squamatus*	92	320	641	0.50	0.96
Cactaceae	*Austrocylindropuntia subulata*	20	48	282	0.17	0.98
Asteraceae	*Baccharis halimifolia*	55	14	106	0.13	1.00
Asteraceae	*Bidens aurea*	41	64	663	0.10	0.91
Asteraceae	*Bidens frondosa*	60	83	341	0.24	0.97
Asteraceae	*Bidens pilosa*	91	21	249	0.08	0.98
Asteraceae	*Bidens subalternans*	69	131	295	0.44	0.99
Poaceae	*Bromus willldenowii*	100	144	403	0.36	0.97
Buddlejaceae	*Buddleja davidii*	43	93	305	0.30	0.98

Family	Species	MRT	CDR	PDR	OCCUPANCY	AUC
Aizoaceae	*Carpobrotus edulis*	104	98	441	0.22	0.97
Poaceae	*Chloris gayana*	102	23	249	0.09	0.99
Asteraceae	*Conyza bonariensis*	132	348	662	0.53	0.95
Asteraceae	*Conyza canadensis*	220	456	803	0.57	0.94
Asteraceae	*Conyza sumatrensis*	100	265	485	0.55	0.96
Poaceae	*Cortaderia selloana*	35	61	335	0.18	0.98
Asteraceae	*Cotula coronopifolia*	107	42	361	0.12	0.97
Solanaceae	*Datura innoxia*	504	62	410	0.15	0.94
Solanaceae	*Datura stramonium*	504	386	744	0.52	0.95
Poaceae	*Echinochloa hispidula*	36	37	242	0.15	0.99
Poaceae	*Echinochloa oryzicola*	104	36	449	0.08	0.98
Poaceae	*Echinochloa oryzoides*	36	28	629	0.04	0.95
Elaeagnaceae	*Elaeagnus angustifolia*	204	54	614	0.09	0.92
Poaceae	*Eleusine indica*	143	43	259	0.17	0.99
Hydrocharitaceae	*Elodea canadensis*	99	13	362	0.04	0.97
Myrtaceae	*Eucalyptus camaldulensis*	204	70	578	0.12	0.95
Myrtaceae	*Eucalyptus globulus*	204	200	317	0.63	0.99
Polygonaceae	*Fallopia baldschuanica*	26	79	757	0.10	0.94
Caesalpiniaceae	*Gleditsia triacanthos*	56	51	364	0.14	0.97
Asclepiadaceae	*Gomphocarpus fruticosus*	242	53	259	0.20	0.99
Boraginaceae	*Heliotropium curassavicum*	130	36	230	0.16	0.98
Asteraceae	*Helianthus tuberosus*	304	179	380	0.47	0.98
Convolvulaceae	*Ipomoea indica*	104	144	381	0.38	0.98
Convolvulaceae	*Ipomoea purpurea*	104	101	553	0.18	0.94
Convolvulaceae	*Ipomoea sagittata*	304	36	235	0.15	0.99
Verbenaceae	*Lippia filiformis*	404	44	490	0.09	0.95
Caprifoliaceae	*Lonicera japonica*	43	70	303	0.23	0.99
Nyctaginaceae	*Mirabilis jalapa*	119	223	438	0.51	0.98
Solanaceae	*Nicotiana glauca*	152	120	425	0.28	0.96
Onagraceae	*Oenothera biennis*	156	100	451	0.22	0.96
Onagraceae	*Oenothera glazioviana*	80	50	446	0.11	0.95
Cactaceae	*Opuntia dillenii*	130	17	421	0.04	0.99
Cactaceae	*Opuntia ficus-indica*	504	396	728	0.54	0.96
Oxalidaceae	*Oxalis pes-caprae*	154	199	437	0.46	0.97
Poaceae	*Paspalum dilatatum*	97	178	441	0.40	0.97
Poaceae	*Paspalum paspalodes*	180	216	568	0.38	0.97
Poaceae	*Paspalum vaginatum*	97	38	239	0.16	0.98
Polygonaceae	*Reynoutria japonica*	30	14	100	0.14	1.00
Fabaceae	*Robinia pseudoacacia*	304	559	768	0.73	0.97
Asteraceae	*Senecio inaequidens*	20	14	609	0.02	0.94
Asteraceae	*Senecio mikanioides*	71	19	141	0.13	0.96
Solanaceae	*Solanum bonariense*	121	42	374	0.11	0.97
Fabaceae	*Sophora japonica*	304	11	97	0.11	1.00
Poaceae	*Sorghum halepense*	204	674	935	0.72	0.95
Poaceae	*Spartina patens*	87	32	186	0.17	1.00

Family	Species	MRT	CDR	PDR	OCCUPANCY	AUC
Poaceae	*Stenotaphrum secundatum*	101	27	230	0.12	0.97
Commelinaceae	*Tradescantia fluminensis*	304	17	601	0.03	0.92
Tropaeolaceae	*Tropaeolum majus*	404	16	315	0.05	0.97
Asteraceae	*Xanthium spinosum*	304	367	694	0.53	0.95
Asteraceae	*Xanthium strumarium*	122	262	530	0.49	0.97
Zygophyllaceae	*Zygophyllum fabago*	143	58	399	0.15	0.96

Appendix II

Maps of present distribution range over potential distribution range for 78 invasive plant species in Spain. (doi: 10.3897/neobiota.12.2341.app2) File format: PDF.

Explanation note: Maps of present distribution range (purple) over potential distribution range (grey) for 78 invasive plant species in Spain. Potential distribution ranges were calculated by niche models as a function of climatic, geographic and landscape variables on the present distribution of species at 10×10 km UTM resolution. Niche models were build by weighted averaging procedures across GLM, GAM, RF and GBM models.

RESEARCH ARTICLE

Geographical, socioeconomic, and ecological determinants of exotic plant naturalization in the United States: insights and updates from improved data

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Abstract

Previous studies on alien species establishment in the United States and around the world have drastically improved our understanding of the patterns of species naturalization, biological invasions, and underlying mechanisms. Meanwhile, relevant new data have been added and the data quality has significantly increased along with the consistency of related concepts and terminology that are being developed. Here using new and/or improved data on the native and exotic plant richness and many socioeconomic and physical variables at the state level in the United States, we attempt to test whether previously discovered patterns still hold, particularly how native and exotic species are related and what are the dominant factors controlling the plant naturalization. We found that, while the number of native species is largely controlled by natural factors such as area and temperature, exotic species and exotic fraction are predominantly influenced by social factors such as human population. When domestically introduced species were included, several aspects in earlier findings were somewhat altered and additional insights regarding the mechanisms of naturalization could be achieved. With increased data availability, however, a greater challenge ahead appears to be how many and which variables to include in analyses.

Introduction

In the past decades, studies on the species naturalizations and invasions in the United States and around the world have drastically improved our understanding of the patterns and underlying mechanisms (e.g., Lockwood and McKinney 2001, Richardson 2011, Simberloff and Rejmánek 2011). Modern ecology continues to have drastic changes partly because of the increased quantity and quality of data and improved analytical technology. For example, studies relating plant species invasions to other biotic (e.g., animal richness), socio-economic, and physical variables demonstrate a remarkable progression in this regard (e.g., various variables used and data interpretations in Stohlgren et al. 2003, Rejmánek 2003, Stohlgren et al. 2006; see also Espinosa-Garcia et al. 2004, Leprieur et al. 2008, Marini et al. 2009, Pyšek et al. 2010, Albuquerque et al. 2011, Bartomeus et al. 2011, Koch et al. 2011, Williamson et al. 2011). Meanwhile, many newly added variables are continuously found responsible for previously observed patterns and processes. As a result, interpretations and conclusions change, sometimes leading to new insights.

On average, in the 48 conterminous US states, about 25% of naturalized plant species are domestically introduced from other states, which significantly increased the exotic richness but simultaneously decreased the earlier reported native richness in each state (Kartesz 2011). For example, out of 865 exotic plant species in North Carolina, 166 are actually introduced from other states but treated as 'native' species in earlier analyzes (for related statements and consequences, see Rejmánek and Randall 1994, McKinney 2005, Guo 2011, and Pyšek 2011). The corrected native and exotic richness data could potentially affect previously revealed relationships and their interpretations (a related issue of data quality and comparability in biological invasions has also been raised by Hulme and Weser 2011). For instance, using a dataset on plant richness in which native and exotic richness were defined using state, rather than national boundaries, Guo and Ricklefs (2010) found that species-area curves (for both natives and exotics) and exotic fraction-area relationships have changed from previously reported results. However, there are several other related aspects that remain unexplored. For example, increased exotic richness and decreased natives richness drastically have increased the exotic fraction (a measure of degree of naturalization or DN) for each state although the corresponding figure for the entire United States does not change. Also, how additional variables (e.g., geographical, social, economical) might be related to the new figures in native vs. exotic richness need to be re-examined. Indeed, when data quantity and quality have been substantially increased with time, it is reasonable and possible to suspect that one may find patterns different from previous studies.

At the state-level, previous studies have examined and found significant effects of native richness, area, latitude, elevation, human population, the time since admission to the Union, and year of publication on the exotic species richness (or exotic fraction) across the United States (e.g., McKinney 2001, Stohlgren et al. 2003, Rejmánek 2003, Guo and Ricklefs 2010). Here, using the dataset provided by Kartesz (2011), we re-examine the effects of several additional variables related to geography (location), biology

(native richness), social-economics, and physical features in each of the 48 contiguous US states to determine factors potentially influencing exotic plant naturalization in the United States (Table 1, S1). We also investigate whether and to what degree the variables involved might be spatially correlated and whether it may make a difference in data interpretation in this particular case.

Table 1. Results from multiple regression analyses showing the relationships between selected land-cover types and the corrected richness of native (a) and exotic (b) vascular plants and the exotic fraction (c) in the 48 conterminous US states (bold-faced *P*-values highlight the significant relationships). Temperature and precipitation represent mean annual temperature (ºC) and mean annual precipitation (cm), respectively. Here, exotic fraction was angular transformed, native and exotic richness, population size, years in the Union, and the number of ecoregions were log transformed, and the rest (mostly related to area) were square-root (sqrt) transformed before analyses.

Source	df	Native richness			Exotic richness			Exotic fraction		
		F-value	*r²*	*P*	*F*-value	*r²*	*P*	*F*-value	*r²*	*P*
Model	11	42.83	0.929	<.0001	19.62	0.857	<.0001	19.75	0.858	<.0001
Error	36									
Corrected total	47									

Variable	df	Parameter Estimate	*t-value*	*P*	Parameter Estimate	*t-value*	*P*	Parameter Estimate	*t-value*	*P*
Intercept	1	2.58451	8.83	**<.0001**	1.45469	1.61	0.116	3.29584	3.74	**0.001**
Exotics	1	0.04626	.50	0.621	--	--	--	--	--	--
Natives	1	--	--	--	0.14878	0.50	0.621	--	--	--
Land area (km²)	1	0.02926	7.05	**<.0001**	-0.01633	-1.46	0.152	-0.00575	-1.53	**0.024**
Population size	1	0.08528	2.28	**0.029**	0.21673	3.50	**0.001**	0.27662	4.57	**0.0001**
Temperature (ºC)	1	0.0767	6.07	**<.0001**	-0.06969	-0.01	0.993	-0.05032	-1.66	0.105
Precipitation (cm)	1	-0.00146	-0.44	0.661	-0.00221	0.37	0.711	0.00578	1.00	0.325
Developed area (km²)	1	-0.00072	-0.86	0.396	-0.002	1.35	0.184	0.00104	0.72	0.474
Cropland (km²)	1	-0.00165	-7.46	**<.0001**	-0.00083	-1.34	0.188	-0.00176	-2.92	**0.006**
Forest (km²)	1	-0.0004	-1.56	0.129	0.00073	1.58	0.124	0.000269	0.60	0.554
Pasture/rangeland (km²)	1	-0.00042	-1.66	0.105	0.00052	1.13	0.266	0.000642	1.42	0.164
Years in Union	1	0.06128	0.55	0.585	0.44498	2.39	**0.022**	0.32045	1.76	0.087
No. Ecoregions	1	0.11397	2.24	**0.032**	-0.05242	-0.54	0.593	-0.01805	-0.19	0.850

Methods

Here we follow the definition of naturalized plant species by Richardson et al. (2000): alien plants that reproduce constantly and sustain populations over many life cycles without direct intervention by humans. Usually, 20 to 60 % of naturalized plant species are invasive species (spreading at considerable distances from parent plants) (Rejmánek 2000a,b, Pyšek et al. 2002). We obtained the exotic and native richness data for plants in each of the 48 conterminous continental US states from Kartesz (2011). This source somewhat overestimates numbers of naturalized species because "exotics"

also include some casual, not completely naturalized species. However, this is the best available approximation of the naturalized species numbers. Kartesz, in the second edition of his "Floristic Synthesis" (2011; see also Guo and Ricklefs 2010), defined exotics based on state boundaries (i.e., with domestic introductions among states included). This improved (or corrected) approach of estimating species richness increased the number of exotic species and at the same time reduced the number of native species compared to previously used figures. To assess the degree of naturalization (DN) in each state, we then calculated the exotic fraction as (exotic species/[native + exotic species]). Even though states are not natural units, we focus on the state-level throughout this study so that comparisons can be made with other state-level studies.

To examine the naturalization patterns related to geography (relative locations of each state), we made a simple comparison between border and interior states. The states with large water (i.e., oceans and the Great Lakes) were defined as border states and the rest as interior states. To examine the possible effects of selected social, economical, and physical variables on the naturalization patterns across the 48 conterminous US states, we related the number of native and exotic species and the exotic fraction to the human population, years since joining the Union, climate condition, the area, land cover types (below), and the number of eco-regions of each state (Bailey 1998). We performed multiple regression analysis to identify the effect of the social, economical and physical factors on the native and exotic richness and the exotic fraction across the 48 states. To elucidate the relationship structure among the selected state variables, we also performed a Principal Component Analysis (PCA). The selected variables were either log (e.g., area) or square root (exotic fraction) transformed to yield approximately normal distributions and to linearize relationships (See Table 1).

The climate data (i.e., mean annual temperature, mean annual precipitation) for each state were obtained from http://www.cdc.noaa.gov/data/usclimate/ (1971-2000) and land cover data from http://www.allcountries.org/uscensus/ (1997). For the land cover data for each state, "developed area" includes urban and built-up areas such as highways, roads, cemeteries, airports, golf courses, landfills, small parks and other transportation facilities. "Cropland" includes both cultivated and non-cultivated lands such as hay fields and horticultural cropland. "Forestland" also includes land stocked by single-stemmed woody species, land of natural regeneration of tree cover, and land not currently developed for non-forest use. "Pastureland/Rangeland" includes land managed primarily for the production of introduced forage plants for livestock grazing and grasslands, savannas, many wetlands, some deserts, and tundra with climax or potential vegetation composed principally of native grasses, forbs or short shrubs suitable for grazing and browsing, and introduced forage species that are managed like rangeland species.

To analyze spatial autocorrelation for all selected variables, we calculated geodesic distances using the latitudinal and longitudinal data based on the center-point of each state. To examine the relative contribution of spatial autocorrelation, we applied and compared the results from both the ordinary-least-squares (OLS) estimation and spatial autoregression analyses (SAR). These two and the PCA analyses were performed

using SAM (Spatial Analysis in Macroecology) (Rangel et al. 2006), which is freely available at www.ecoevol.ufg.br/sam.

Results

In contrast to previously reported significant relationship between native and exotic species richness estimated based on the US boundary, using the corrected values (i.e., species truly native or exotic to each of the 48 states, rather than to the entire continental US), the relationship became non-significant (Fig. 1). The states with higher foreign exotic richness or fraction also had higher domestic exotic species richness or fraction (r^2 = 0.83, p < 0.0001).
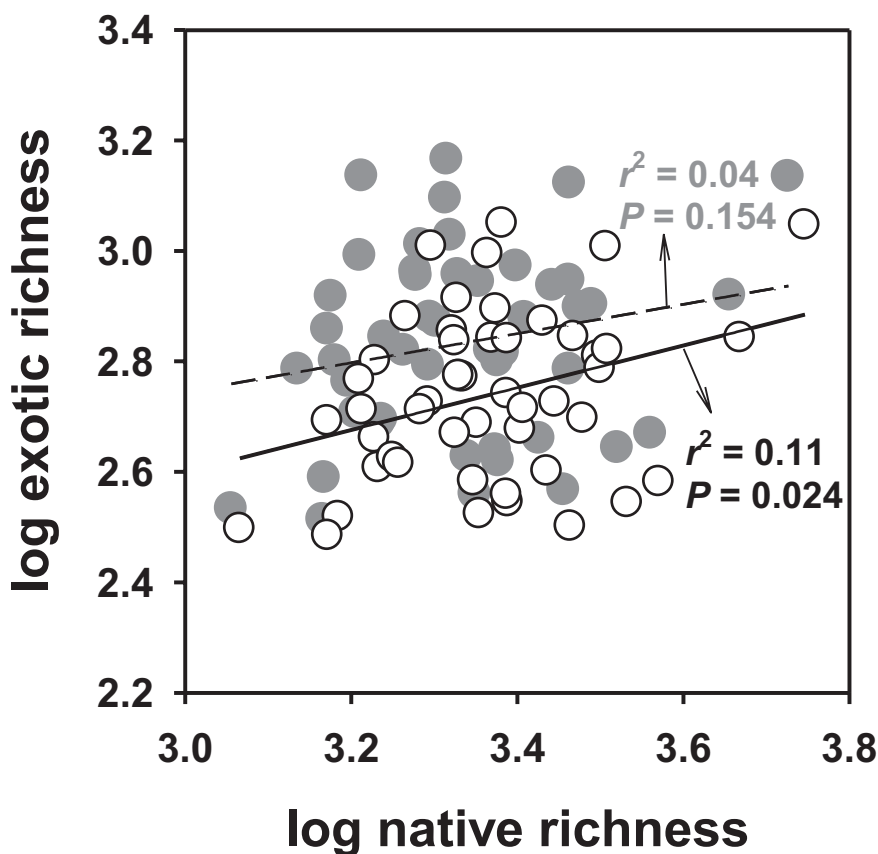

Figure 1. An example showing how the improved data of native vs. exotic species had altered previously described patterns of species naturalization in the United States. Using corrected values (i.e., species truly native or exotic to each of the 48 states, rather than to the entire continental United States), the relationship between native and exotic species richness became non-significant as indicated by the solid dots and dashed regression line. This result is in direct contrast with the previously reported significant relationship (open circles and solid regression line).

Analyses using the improved naturalized (Kartesz's "exotic") and native richness data across the 48 continental US states showed geographic (isolation) effects; i.e., although there was no difference in native richness between the border (coastal) states (with isolation on part of their borders) and interior states, the former had higher exotic richness and fractions than the latter (Fig. 2a). The exotic fraction decreased with state area but the declining rate was significantly higher for the interior states than for the border states (Fig. 2b; t = 3.79, P < 0.001). The top five states in the conterminous continental United States with the highest exotic fractions were all border states with rather small areas such as Massachusetts (84%), New York (71%), Pennsylvania (61%), Connecticut (60%), and Maine (55%) in the Northeast; whereas the ones with the lowest exotic fractions were the ones in the relatively dry and interior areas such as Arizona (13%), Nevada (13%), New Mexico (13%), Wyoming (16%), and Colorado (17%). In addition, our data show that the border states also have higher proportions of domestic exotics (i.e., domestic exotics/ all exotics = 22%) than the interior states (15%; chi-square test, df = 1, P < 0.001).

Native richness was positively related to land area, temperature, human population size, and the number of ecoregions (as a measure of habitat diversity), but negatively related to the area of crop lands. By contrast, exotic species and exotic fraction were predominantly influenced by social factors (i.e., human population size). Exotic richness was also positively related to the number of years since joining the Union, and exotic fraction was also negatively affected by land area (Guo and Ricklefs 2010) and cropland (marginally; see Table 1, S1). Again, not surprisingly, both domestic and foreign exotic plants showed similar relationships with selected biotic, social/economic, and physical factors (not shown).

Results from PCA that extract orthogonal axes depicted a strong correlation structure (collinearity) among the selected state variables for the 48 conterminous continental US states. Several independent variables such as the number of ecoregions, human population size, pasture/rangeland, and urban area were positively related to each other and related to the response variable, native richness, along the first (horizontal) axis. Independent variables such as years in the Union and human population size were also positively related to each other and related to the exotic richness and exotic fraction (Fig. 3). The first component principal accounted for 37% of the total variance and the first two components (out of 13) accounted for 64% of the total variance. All variables except human population size were strongly correlated over space, but at different distances (Fig. S1). The state land area showed positive autocorrelations over the shortest distances and the number of eco-regions showed positive autocorrelations over the smallest distances, with other variables at intermediate distances. Interestingly, the exotic richness (and exotic fraction) exhibited significant positive spatial autocorrelation at a larger distance than native richness, suggesting greater homogenization (or similarity) in terms of species exotic floras across the 48 states than that in native floras (see also Rejmánek 2000b). However, as the distance continue to increase, the native richness, exotic fraction, land area, the number of eco-regions, and precipitation exhibited significant negative autocorrelations at the farthest distance; whereas the forestland, cropland, paster/range, temperature, and exotic richness exhib-
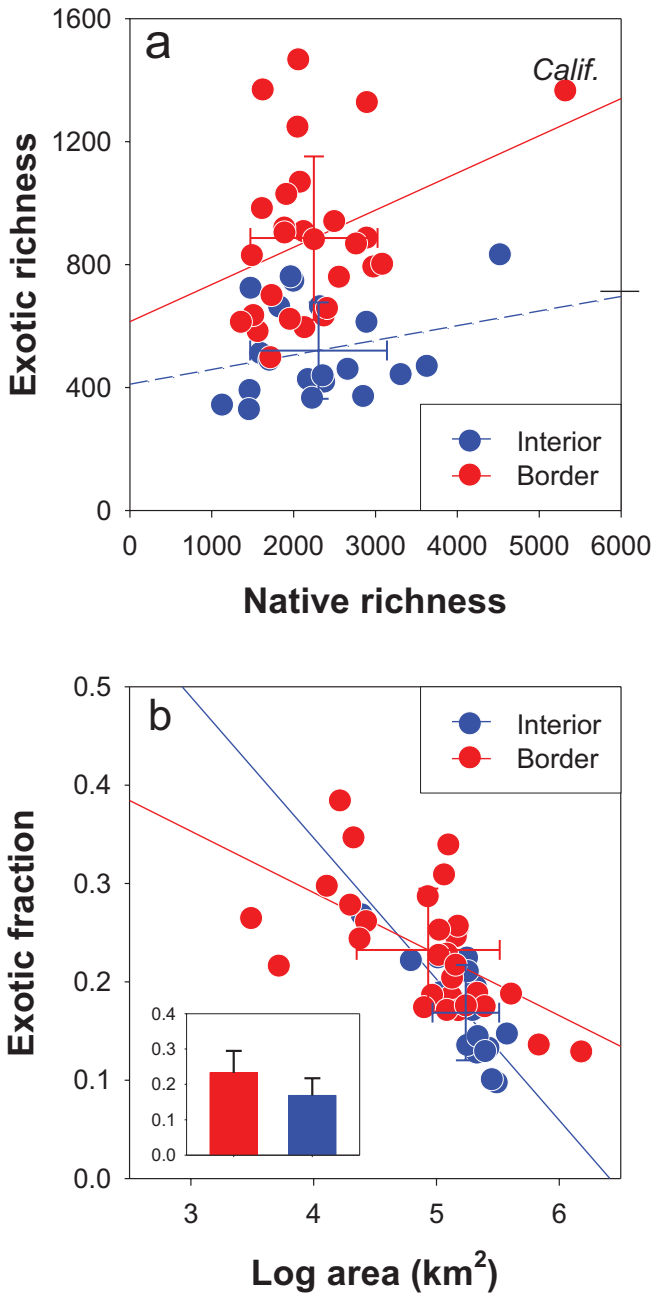
Figure 2. An example of geographical effects on the native and exotics richness in the conterminous continental United States. There was no significant difference in native richness between the border and interior states of the US but the border states showed significantly higher exotic richness and fraction than the interior states (*t* - test, *P* < 0.05). The exotic fraction decreased with state area and the interior states showed a greater decline. Here, natives and exotics were estimated using states own borders (bi-directional bars = SD).
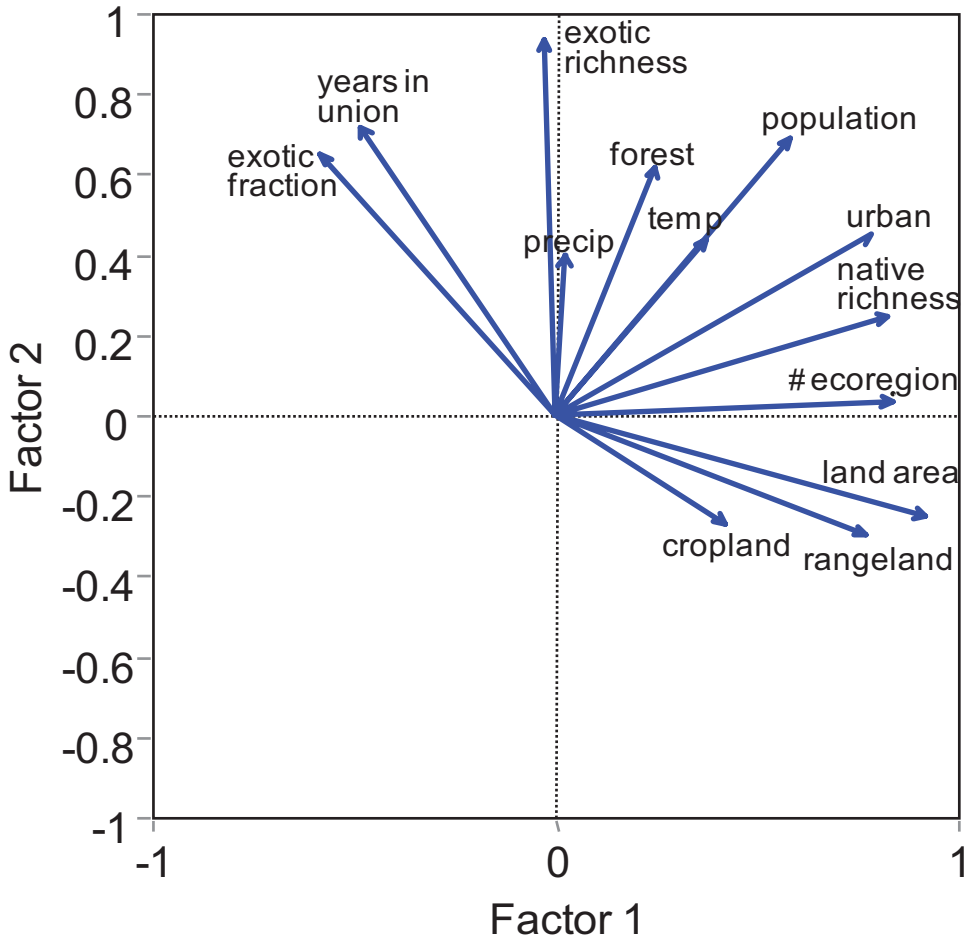
Figure 3. Results from Principal Component Analysis (PCA) that extracts orthogonal axes and shows the two-dimensional (PC1 and PC2) correlation structure among the selected state variables for the 48 conterminous continental US states. Here, "temp" represents temperature (ºC) and "precip" represents precipitation (cm).

ited U-shaped spatial autocorrelations, which may indicate a scenario similar to "one big patch" (i.e., the values are all significant and positive at short and large distances but negative at intermediate) proposed by Fortin and Dale (2005) (Fig. S1).

To test the relative strength of spatial autocorrelation, which was measured based on the geodesic distances among the 48 states, we performed ordinary-least-squares (OLS) estimation and spatial autoregression analyses (SAR) that took both predictor variables and space (autocorrelation) into account. We then compared the results through both approaches. AICc values indicated that OLS (ordinary least squares multiple regression analysis) produced the best fitted models for native and exotic species richness and for exotic fraction (Table S1), despite the contributions from spatial autocorrelation in certain variables.

Discussion

In agreement with several previous studies (Rejmánek 2003, Stohlgren et al. 2006), the new results demonstrate the critical aspects of choosing independent variables in drawing conclusions; that is, adding or removing certain variables, due to either data availability or author discretion, can influence results and data interpretation. It is understandable that, in some cases, one or more variables are not analyzed owing to lack of data, although this might lead to biased explanations regarding the mechanisms underlying observed patterns. Indeed, the variables in ecological analyses are often constrained by data availability rather than author discretion. As Rejmánek (2003) showed, when certain variables are added or removed, the conclusions can sometimes change drastically. Increased data availability poses challenges for choosing variables and analytical tools in data analysis. For example, when temperature is considered a potentially important factor, choices must be made between using mean annual temperature, temperature in the warmest/coldest month (or quarter), degree days of temperature above or below certain level, and extreme temperatures. Some of the temperature variables might show significant relationships with the dependent variables while others may not. Similarly, there are many variables associated with human activities (e.g., population size/density, road density, energy consumption) that are interrelated to each other and each may show a different level of responsibility for the observed patterns of biotic invasions (e.g., Lin et al. 2011).

The border states are partly isolated from other interior states therefore should lose accessibility by some domestic exotics, but should have greater accessibility by foreign exotics through proportionally more and larger international airports and sea ports and earlier encounter of foreign sources of propagules (Koch et al. 2011). However, surprisingly, our data show that the border states still have higher proportion of domestic exotics. It remains puzzling how this paradoxical pattern has emerged. It is possible that domestic traffic (travel, trade) among the border or coastal states and from interior states to border states still exceeds traffic among interior states, but further examination of this phenomenon is clearly needed.

While the number of native species is related to both natural and social variables, exotic richness and fraction are predominately influenced by human factors (see also Pyšek et al. 2010). The factors related to native richness are readily interpreted: larger area through the species-area effect; human populations achieve greater density in more productive and heterogeneous areas that also support richer native flora (McKinney 2001, Rejmánek 2003); warmer, more southern latitudes typically support more species; crop lands diminish the area of native habitat. In contrast, influences on exotic species richness and the exotic fraction are more complex but mostly related to social-economic activities. The positive effect of human population on the number of exotic species and exotic fraction is likely associated with the primary sources and points of introduction in the United States (e.g., Blackburn and Duncan 2001 for birds; Gavier-Pizarro et al. 2010 for plants; Table 1, S1). The negative effect of state land area may be due to reduced pool size of domestic exotics; that is, the larger the

state, the smaller outside domestic exotic species pool within the United States (Guo and Ricklefs 2010). Also, in general, smaller states were admitted to the Union earlier, and their history of intensive disturbance and species introduction was therefore longer (Rejmánek 2003). The strong relationship between foreign and domestic exotic richness might indicate that domestic and foreign exotic plants exhibit similar patterns and mechanisms of naturalization across the 48 United States despite the different sources of exotics.

Two major issues deserve attention. First, it would be reasonable to argue that at least some of the differences in previously described patterns of species invasion or naturalization even from the same focal habitat or area stem either from inconsistent definition or inconsistent practice in regarding how to "correctly" count 'exotics'. As Hulme and Weser (2011) point out, a greater challenge ahead is how to ensure data quality and to standardize the data collected from different habitats and regions so that accurate and meaningful comparisons can be made. To date, many large databases have not distinguished between "domestic" and "foreign" exotic species (Guo 2011). Recent moves to increasingly connect disparate databases of variable quality without some consistent quality control may lead to erroneous conclusions (Hulme and Weser 2011, Pyšek 2011).

Second, increased data availability often leads to data dependency over space, time, or both, thus to violation of the assumptions of many statistical tests. It is still not clear whether, and to what extent, spatial or temporal autocorrelation and collinearity contribute to the inconsistency in earlier studies. In our particular case, spatial autoregressions confirm the results from multiple regressions and increase confidence in data interpretation. The OLS and SAR gave consistent results (Table S1), suggesting that the explanatory variables are also spatially autocorrelated (see Fig. S1). Thus, removing any autocorrelation among the explanatory variables would also remove most of the explanatory power of the explanatory variables. Unlike the native or exotic richness and exotic fraction, the residuals of most variables do not exhibit spatial autocorrelations (V. Jarosik, Personal Communications; see also Dormann et al. 2007, Pyšek et al. 2010). Therefore, in agreement with findings by social scientists at the state-level by Wasserman and Stack (1995), spatial autocorrelation does not seem to be a serious problem in our analyses at the state scale. However, the spatial autocorrelations of different variables over varied distance intervals do offer additional details regarding their spatial patterns and could potentially reflect the effects of underlying ecological gradients.

The multiple regressions confirm both positive effects of human population size on exotic species richness and exotic fraction, in the United States. Collinearity seems a greater statistical challenge than spatial autocorrelation. However, neither collinearity nor spatial autocorrelation seem to affect the overall results in this particular case. Nevertheless, knowing how the selected variables are spatially or temporally correlated might be informative, as they could affect the response variable interactively. When strong collinearity is detected, significantly reducing the number of variables would be an easy fix for collinearity but, at the same time, information and insights may be

lost when ecological processes are influenced by additional factors than those selected. Further, adding more variables offers potentially more hypotheses and tests, and more detailed interpretations.

In summary, using newly added and improved data provides new insights regarding the plant naturalization mechanisms across the United States. All previously used independent variables at state-level analyses such human population, area, were also found significantly related to native and exotic plant richness. Yet, when additional variables were added, we found more variables that were significantly related to native and exotic richness and exotic fraction. Also, in this particular study at the state level, different statistical methods adopted here produced remarkably similar results regardless spatial correlation. However, a greater challenge ahead is how to properly handle greater numbers of variables with increased data availability, and caution is needed when dealing with data at other spatial scales (e.g., county-level).

Acknowledgments

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Supplementary Material

Table S1. A sample of comparative results from the ordinary-least-squares (OLS) estimation and spatial autoregression analyses (SAR). Here we examined the effect of land area (km^2) and its spatial autocorrelation (i.e., "space") on exotic fraction, and native richness, and exotic richness. SAR on other variables showed very similar results in terms of the role of spatial autocorrelation (not shown).

	Native richness (log_{10})		Exotic richness (log_{10})		Exotic fraction	
		AICc		AICc		AICc
OLS						
r^2	0.416	-73.099	0.071	-28.398	0.466	-42.580
Constant(t)	64.959***		47.284***		-4.880**	
Land area (t)	5.286**		-0.536		-3.252*	
SAR						
Land area (r^2)	0.416	-73.099	0.037	-26.652	0.386	-35.868
Land area + space (r^2)	0.449	-75.884	0.058	-7.704	0.406	-37.466

* $P < 0.01$, ** $P < 0.001$, *** $P < 0.0001$.
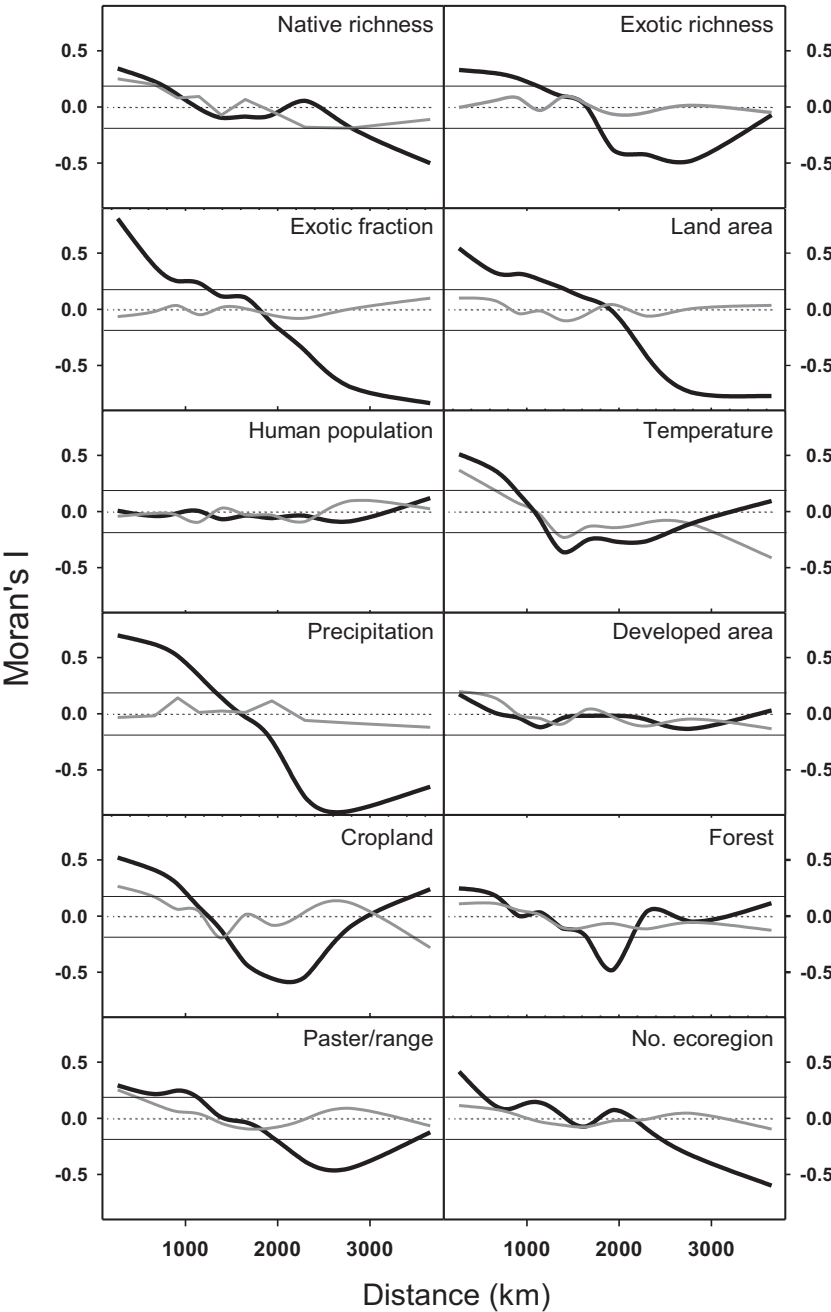
Figure S1. Spatial autocorrelation coefficient (Moran's I) of species richness, exotic fraction, and other state variables (black line) and their residuals (gray lines) across the 48 conterminous continental US states. The data points above and upper or below the lower horizontal lines in each panel indicate significant spatial autocorrelations based on randomization (i.e., *P* < 0.05), using the Monte Carlo randomized data (distances; 200 replicates). For most variables, residuals do not show spatial autocorrelation (see Dormann et al. 2007).

REVIEW ARTICLES

Insights into invasion and restoration ecology: Time to collaborate towards a holistic approach to tackle biological invasions

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Abstract

The aim of our study is to provide an integrated framework for the management of alien plant invasions, combining insights and experiences from the fields of invasion and restoration ecology to enable more effective management of invasive species. To determine linkages between the scientific outputs of the two disciplines we used an existing data base on restoration studies between 2000 and 2008 and did a bibliometric analysis. We identified the type of restoration applied, determined by the aim of the study, and conducted a content analysis on 208 selected studies with a link to biological invasions (invasion-restoration studies). We found a total of 1075 articles on ecosystem restoration, with only eight percent of the studies having the main objective to control alien invasions. The content analysis of 208 invasion-restoration studies showed that the majority of the studies focused on causes of degradation other than alien invasions. If invaders were referred to as the main driver of degradation, the prevalent cause for degradation was invaders outcompeting and replacing native species. Mechanical control of alien plant invasions was by far the most common control method used. Measures that went beyond the removal of alien plants were implemented in sixty-five percent of the studies.

Although invasion control was not as common as other types of restoration, a closer look at the sub-group of invasion-restoration studies shows a clear link between restoration and invasion ecology. Concerns, as identified in the literature review, are firstly that restoration activities mostly focus on controlling the invader while other underlying causes for degradation are neglected, and secondly that the current approach of dealing with alien invasions lacks a combination of theoretical and practical aspects.

We suggest that closer collaboration between invasion and restoration ecologists can help to improve the management of alien plant invasions. We conclude with a framework and a case study from Perth Western Australia integrating the two disciplines, with the aim of informing restoration practice.

Introduction

Management of invaded ecosystems is an increasingly complex problem worldwide (e.g. Roura-Pascual et al. 2009). It has been acknowledged that clearing of invasive species alone is often not sufficient for re-establishing native communities; therefore some form of restoration is increasingly seen as vital when dealing with alien invasions (Esler et al. 2008). However, restoration efforts are challenged by numerous obstacles caused by invasive species such as altered ecosystem properties and ecosystem functions. Consequently, restoration efforts often have unexpected outcomes or even unforeseen negative consequences (Zavaleta et al. 2001).

In this study we attempt to find ways of improving the management of alien plant invasions by combining insights and experiences from the fields of invasion and restoration ecology with the aim of informing restoration practice. To tackle the challenge of combining efforts from both fields we first need to understand whether, how and where the two disciplines overlap in terms of applied management. We therefore begin our study with a literature analysis looking at restoration studies with a link to biological invasions. Building on the findings of our literature analysis we provide an integrated framework for the management of alien plant invasions. We focus on plant invasions only as these represent the primary challenge in terrestrial restoration ecology.

Restoration ecology and invasion ecology can be seen as synergistic disciplines with many similarities and cross cutting debates. They both originated in the mid -20th century and are considered relatively new disciplines in the field of ecology. Both are applied, focusing on conservation and management issues (Hobbs and Richardson 2011) but not without controversy (Vince et al. 2011, Davis et al. 2011, Lambertini et al. 2011, Simberloff et al. 2011).

Dealing with invasive alien species is one of the key elements for ecosystem restoration (D'Antonio and Meyerson 2002). The removal of invasive alien species is often conducted to achieve goals other than just the control of the invader (e.g., to improve ecosystem function and/or services or conserve or reduce biodiversity loss) however, more and more restoration projects define the removal of alien species as a goal in itself (Hobbs and Richardson 2011).

Invasion ecologists have been criticised for being detached from the practicalities of dealing with invasive species management (Richardson et al. 2004, Shaw et al. 2010) and for making little progress in reducing negative impacts of invasions (Hulme 2003)

while restoration ecology has been criticised for focusing too much on the symptoms of ecosystem degradation (e.g., controlling the invader without manipulating abiotic and biotic ecosystem components), thereby neglecting to consider the causes for ecosystem damage (Buckley 2008), which in some cases resulted in wrong assumptions and ineffective approaches (Hobbs and Richardson 2011).

In summary, restoration ecology and invasion ecology can be described as synergistic disciplines which share similarities but also differ in aspects and which both have been criticised for certain shortcomings. We therefore suggest that a combined effort between invasion and restoration ecologists of sharing and interpreting knowledge, conducting research and applying the results to management and restoration of ecosystems could improve our understanding of biological invasions. We further suggest that understandings from invasion ecology could inform restoration activities to increase their effectiveness while reducing the impacts of invasive species leading to more resilient restored ecosystems. The "perfect world" scenario would be if invasion ecology could provide insights incorporating theoretical knowledge into management scenarios, while delivering information on the causes and consequences of ecosystem degradation. On the other hand restoration ecology could (on the basis of these insights) deliver more effective solutions to these problems, while embedding the work in a stronger theoretical context.

To elucidate the link between restoration and invasion ecology and to provide a basis for our framework, we ask the overarching questions: To what extent is the link between restoration and invasion ecology reflected in the scientific literature? What role do biological invasions play in ecosystem degradation, how do they influence the success of restoration activities and how can restoration benefit the management of alien plant invasions?

More specific questions are:

1. How many restoration studies published between 2000 and 2008 have invasion control as an explicit aim and how do these studies rank in comparison to other types of restoration (i.e. forest restoration or wetland restoration)?
2. How many restoration studies have a link to biological invasions (from hereon referred to as invasion-restoration studies) and is there a primary geographic focus (country and ecosystem) of invasion-restoration studies?
3. How many invasion-restoration studies investigate the outcomes of restoration projects conducted by practitioners and how many studies give recommendations for restoration? If recommendations are given, were these accounted for in restoration actions?
4. How many studies investigate invasive species as a main driver of degradation (causes for degradation) and, if invasive species are only symptoms of degradation, which other drivers have been identified?
5. If invaders are referred to as only cause for degradation, which negative effects are viewed as responsible for the degradation (e.g. nutrient enrichment, competition for resources)?

6. Which percentage of the invasion-restoration studies have invasion control as an explicit aim and what is the adopted approach for remedy (invasion control measure, e.g. herbicide application and burning)?
7. Which percentage of studies implement measures that go beyond the removal of alien plants, what are the reasons for taking additional steps and do studies report long term success?
8. If the study has other objectives (e.g. forest restoration) and invasion control is not the explicit aim, how do invaders influence the success of restoration activities?

Based on the results of our literature analysis, we identify general concerns and methodological gaps. We then develop a framework incorporating ecosystem interactions and invasive species into restoration planning and goal setting. To illustrate the relevance of our framework we conclude with a case study utilising the framework in restoration projects in the Canning River, Perth, south-western Australia.

Methods

Terminology followed Pyšek et al. (2004), referring to an alien as "a plant taxa in a given area whose presence there is due to intentional or accidental introduction as a result of human activities" and to invasive as "naturalized plants that produce reproductive offspring, often in very large numbers, at considerable distances from parent plants, and thus have the potential to spread over a considerable area". As synonyms for the term alien we identified exotics, non-native species, introduced species and non-indigenous species. The term restoration is used following the definition of the Society for Ecological Restoration (SER 2004) as "the process of assisting the recovery of an ecosystem that has been degraded damaged or destroyed" and as a synonym we identified rehabilitation.

For the literature search we used two different sources. Firstly, we used an existing data base on restoration studies for the years 2000 - 2008 (for more details see Aronson et al. 2010). Secondly we searched the ISI web of science for papers using the term invasion and its derivates, excluding conference proceedings, refined the results with ecology as "subject area" and searched for restoration and rehabilitation. We then defined 17 key journals in invasion ecology (Pyšek et al. 2006) and restricted our analysis to these journals (Appendix S1). We excluded "grey literature" although we are well aware that many restoration studies are only published in the form of reports or popular articles and acknowledge that this is a shortcoming of our study.

We found a total of 1075 articles on ecosystem restoration that included (but were not limited to) those linked in some way to alien invasion. Analysing these papers, we identified the type of restoration with 10 different restoration types ranging from forest and wetland restoration to restoration after alien invasion. We determined the type of restoration by the main aim of the study, which means that for example a restoration

project taking place in a wetland which is invaded by alien species with the aim of controlling the invader was classified as "restoration after alien invasion" (Appendix S2).

Second, we selected all restoration studies with a link to biological invasions on the basis of the presence of key terms and their combinations occurring in title, keywords and abstract. The resulting 208 studies are from here-on referred to as invasion-restoration studies and include all studies that mention biological invasions; hence they include (but are not limited to) studies that are aiming to control the invader. We conducted a content analysis (Babbie and Mouton 2001) of the 208 articles: The latent content or underlying meaning of the articles was coded by reading each article and making an assessment of its overall emphasis according to a predetermined list of variables (Appendix S3). The variables were selected to examine the current practise of tackling alien invasions. We selected criteria to identify the objective and geographic focus of the study, the adopted approach for remedy (restoration approach and invasion control measures), and the reason for intervention (causes of degradation).

Results

The importance of invasion control for restoration studies

We examined 1075 restoration studies in 62 countries. An overall comparison showed that the aim 'invasion control' globally ranks fourth (90 studies, 8 %) after forest, wetland, and species restoration. Except for Europe, all continents have a clear bias towards forest restoration. Africa is the only continent on which invasion control ranges second after forest restoration with 16 % of the restoration studies having the main objective to control alien invasions. In Asia and Central America forest restoration plays by far the most important role (40 % and 68 % of all studies), whereas no study on invasion control was recorded in our database. In North America and South America invasion control ranges third (12 % and 8 % respectively) after forest restoration and wetland restoration. For Central America no study on invasion control was recorded in our data base. In Europe invasion control was only included in three percent of the studies. In Oceania (New Zealand, Australia and Hawaii) invasion control ranks fifth (8 %) (Figure 1).

Invasion-restoration studies characterised

Of the 1075 studies investigated 208 (19 %) had a link to biological invasions (invasion-restoration studies). More than 50 % of all invasion-restoration studies have been conducted in the USA (134 studies). The other 50 % have been conducted in Europe (27 studies), Australia (14 studies) and Canada (11 studies). Africa and South America are only represented in six and three studies respectively. Thirty percent of the studies focus on grassland ecosystems, 16 % on forest ecosystems and 14 % on wetlands.
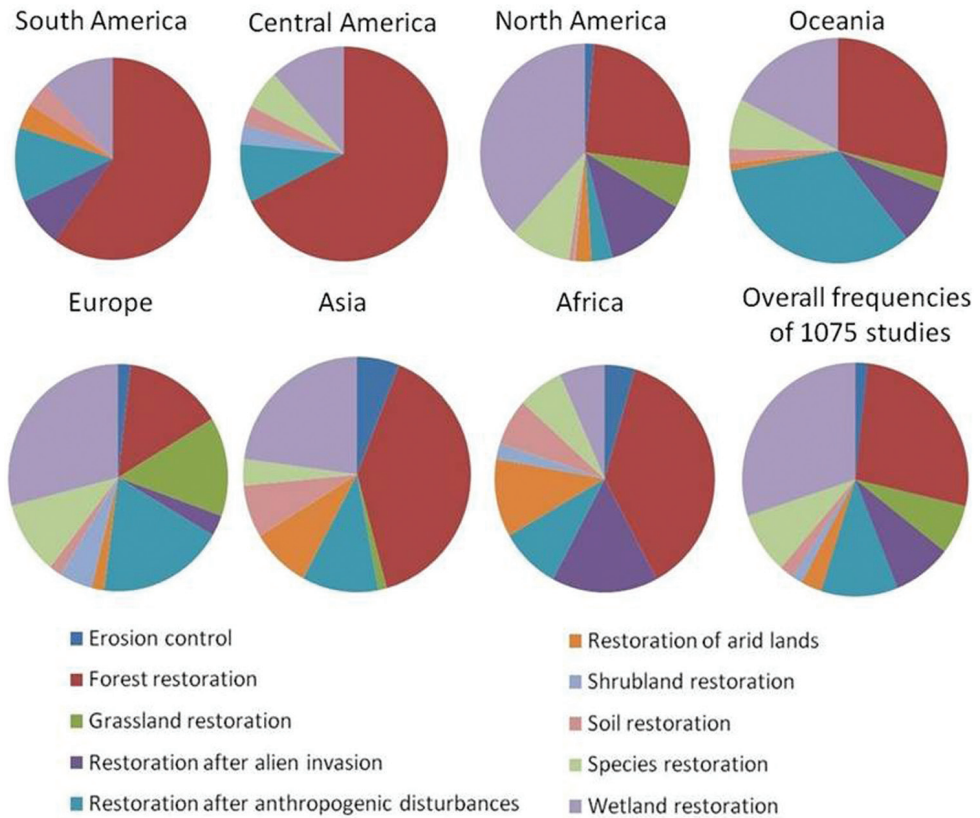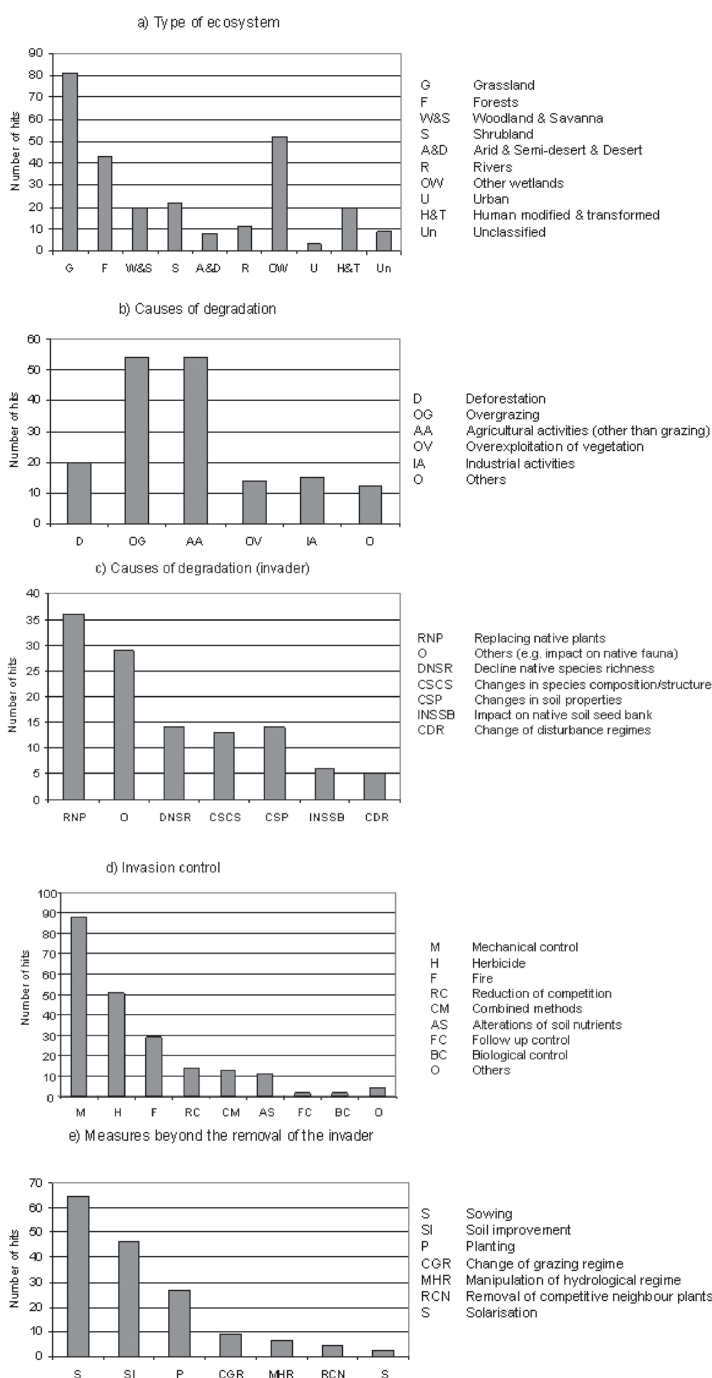
Figure 1. Types of restoration in different geographic regions of the world. Restoration types in different geographical regions identified in a literature analysis of 1075 restoration studies.

Other ecosystems under study are shrublands (8 %), woodlands and savanna (18 %) and human modified ecosystems (7 %) (Figure 2a).

Seventy-six percent (158 studies) of the invasion-restoration studies were empirical studies including restoration experiments but also other experiments (e.g. competition or impact studies). The results below refer to the empirical studies.

Thirteen percent of the empirical studies investigated outcomes of restoration projects conducted by practitioners (compared to pure scientific restoration experiments) and several studies did provide recommendations for restoration, however, only one study reported on scientific results that were directly translated into restoration actions.

Thirty-two percent of the empirical studies referred to alien invasion as main cause for degradation whereas 52 % of the studies referred to alien invasions as a symptom of degradation. Other prevalent causes for degradation were overgrazing and agricultural activities (each 32 %), deforestation (12 %), overexploitation of vegetation (8 %) and industrial activities (9 %) (Figure 2b). Invasive native species were the subject of ten percent of the studies with four studies referring to native invasions as cause for degradation and 16 studies referring to native invasions as symptom of degradation.

Figure 2. Restoration studies with a linkage to biological invasion (invasion-restoration studies) in different categories. **a** Ecosystem types **b** causes of degradation **c** causes of degradation by the invader **d** measures of invasion control and **e** measures adopted beyond the removal of the invader as reflected in a literature review of 208 publications with a link to biological invasions (invasion-restoration studies).

If invaders were referred to as the main driver of degradation, the prevalent cause for degradation was invaders outcompeting and replacing native species (58 %). Other causes for degradation were a decline in native species richness (23 %), a change in species composition or structure (21 %), the depletion of the native seed bank, changes in soil properties or resource availability (11 %), an increase in litter (11 %) or a change in disturbance regimes (8 %) (Figure 2c).

Sixty-three percent (101) of studies had the overall objective to control invasive species and/or to promote native species. Other objectives included restoration of degraded sites (10 %) and forest restoration (7 %). The rest of the studies investigated the impact of invaders on the native ecosystem (11 %), looked at competition between native and alien plant species (8 %), or at costs and benefits of restoration (economic study) (1 %).

If invasion control was the explicit aim of the study, the main measure adopted was mechanical control (33 %) followed by herbicide application (19 %). Other common approaches of invasion control were burning (11 %), alteration of soil nutrients (11 %) or a combination thereof (13 %). Follow-up methods or biological control measures were only adopted in two studies (Figure 2d).

Sixty-five percent of the studies, which had the overall aim to control invaders and promote natives, implemented measures that went beyond the removal of alien plants. The most prevalent measure adopted was re-introducing native plant species by sowing (64 % of the studies) followed by soil improvement (47 %) and planting of desirable native species (27 %). Other measures adopted were change of grazing regime (9 %), manipulation of hydrological regime in riparian ecosystems (7 %), and removal of competitive neighbor plants (4 %) (Figure 2e). Reasons for additional measures as described by the authors were lack of native species establishment (44 %) and/or depleted native seed bank (4 %), or competitive advantage of the invader (e.g. through elevated nutrients) (20 %). Some studies adopted additional measures to prevent alien species spread or reduce the susceptibility of the site to invasions (11 %). Others described the system as "resistant to restoration" because of positive feedback loops established by the invader for example in connection with a change in the fire regime (11 %). Eleven percent of the studies justified additional measures because the site was highly degraded (e.g. soil contaminated with pesticides and fertilizer).

Twenty-two percent of the studies reported on long-term success of which nine percent were successful, eleven percent were partly successful and two percent were described as not successful.

If invasion control was not the explicit aim of the study, invaders were described as influencing the success of restoration activities through a dominance of the invader either after active restoration (36 %) or before restoration, hindering the establishment of native species (18 %). On the other hand alien species were used for restoration of degraded sites in 18 % of the studies or were used to facilitate the establishment of native species (e.g. in forest restoration) (18 %).

Discussion

An overall comparison of published restoration studies revealed that invasion control is not as common as other types of restoration (e.g. forest restoration). However, a closer look at the sub-group of invasion-restoration studies shows a clear link between invasion and restoration ecology in the scientific literature. The importance of restoration for the management of alien plant invasion is reflected in our finding that 65% of the studies with the aim of controlling the invader and promoting native species adopted measures other than the removal of the invader. At the same time, invasives play an important role in restoration studies that have other objectives (e.g. forest restoration), interfering with restoration actions by hindering the establishment of native species. Interesting is the finding that in some cases alien species are even used in the process of restoration (Lavoie et al. 2005, Jurado et al. 2006).

To find ways of improving the management of alien plant invasions we sought to identify "shortcomings" of invasion-restoration studies that could be overcome by combining efforts of invasion and restoration ecologists. The majority of the restoration studies focusing on alien invasions report causes of degradation other than alien invasions. This finding reflects a very important issue concerning the management of alien plant invasions, that invasions are often considered a symptom rather than a cause of degradation (MacDougall and Turkington 2005). The consideration of not only the invasive species but the whole ecosystem context with its multiple interacting factors during restoration activities provides a number of potentially different management and restoration options (Firn et al. 2008). For example, as shown in our results, changes in soil nutrient properties are viewed as a main cause for degradation through alien invasion. Restoration measures to address this problem include either reduction or addition of soil nutrients in an attempt to reverse the disturbance to the ecosystem. This nutrient change to the ecosystem, however, may in fact only be symptomatic of other changes within the ecosystem (Suding et al. 2004, Fisher et al. 2009a, Fisher et al. 2009b).

Another example is competition by invasive plant species. Competition was by far the most frequently investigated process of ecosystem degradation caused by the invader and the most commonly adopted measure to address this problem was the removal of the invader. However, the removal of alien plant species alone often does not have lasting and effective outcomes, with differing removal methods having the potential to provide different responses and interactions within the managed/restored native plant community (Flory and Clay 2009). Firstly, the removal of invasive species alone might not allow ecosystems to recover as some invaders leave behind legacies which change the condition of the habitat preventing native species from recolonisation (Zavaleta et al. 2001, Fisher et al. 2006, Fisher et al. 2009b) and or promoting secondary invasions (Galatowitsch and Richardson 2005, Beater et al. 2008). Secondly, restoration efforts can have unforeseen consequences that exacerbate rather than mitigate the problem that initiated the restoration effort (Hobbs and Richardson 2011).

These examples show that restoration actions designed specifically to mitigate the known change may neglect other co-existing alterations to the ecosystem state, leading to unexpected results such as replacement by a new alien species, or deaths of reintroduced native species (Vilà and Gimeno 2007, Beater et al. 2008, Blackburn et al. 2009, Bergstrom et al. 2009).

The finding that mechanical control of alien plant invasions is by far the most common control method is also surprising as it is presumably also the most expensive. Nuñez and Pauchard (2010) argue that developed countries are in the position to allocate funds for sophisticated control methods, while developing countries might have fewer funds but abundant low cost labour, which is a major advantage. On the other hand Kull et al. (2011) and Wilson et al. (2011) state that control of alien invasions in developing countries is often in direct conflict with uses of invasives (e.g., for restoration of degraded lands or as a resource for poor communities).

Surprising is that follow-up control and measures of biological control were only adopted in two studies respectively. Invasive species are often characterised by high propagule pressure therefore follow-up controls are essential to prevent re-invasion and should therefore be included into restoration projects (Gaertner et al. 2012).

Our findings show that there is an established link between restoration and invasion ecology, however our results also show that the management of alien plant invasion and restoration after alien invasions respectively could be improved. Although the majority of the studies identified invasive species as symptoms of habitat degradation rather than cause, restoration activities mostly focused on controlling the invader while other underlying causes for degradation were neglected. Here a focus on the causes of degradation rather than symptoms will increase the efficiency of restoration efforts (Vilà et al. 2011).

As reflected in our results, another concern with the current approach of dealing with alien invasions for both fields is the limited combination of theoretical and practical aspects. This deficiency leads to difficulties in translating theoretical concepts into effective management actions. The "knowing-doing gap" between knowledge acquisition and its implementation has been the subject of recent discussion in different fora, mainly conservation practice disciplines (e.g. Knight et al. 2008) and has also been verified for the field of invasion ecology (Esler et al. 2010, McGeoch et al. 2010, Richardson et al. 2010, Shaw et al. 2010).

We believe that the identified shortcomings could be addressed by closer collaboration between restoration and invasion ecologists including practitioners. In the next paragraph we present a nine-step framework focusing on invasion management in nine steps integrating restoration and invasion ecologists and practitioners.

An integrated framework for the management of alien plant invasions

In Figure 3, we present an integrated framework for an improved management of alien plant invasions based on the findings of our literature analysis. Our framework incorporates ecosystem interactions and invasive species into restoration planning and goal set-

ting (Norton 2009, Palmer and Filoso 2009). This inclusion will provide the opportunity to better integrate invasion and restoration ecology (Firn et al. 2010, Traveset and Richardson 2010, Hobbs and Richardson 2011), which will potentially result in more effective restoration projects with successful management of invasive species (Figure 3).

Firstly, it is important to decide whether restoration management interventions beyond the removal of alien plants are necessary. If ecosystem processes and function are altered, restoration actions beyond the removal of the invader will likely be necessary. In this case restoration and invasion ecologists will need to consider the causes of degradation and resultant ecosystem changes when setting goals, aims and measurements of success for the restoration project (Figure 3, Step 1-3). Once restoration strategies and research methods have been developed (Step 4) practitioners should be involved to develop restoration actions (Step 5). Before and after restoration it is crucial to collect scientific data to investigate species interactions, the effects of disturbances and results of restoration actions (Step 4 and 7). Results of ecological scientific surveys before and after restoration will provide understandings of interactions and evidence to adapt and modify restoration activities as ecosystems respond to management changes (Figure 3 step 6 -8). In the next section we introduce a case study focussed on restoration projects in the Canning River, Perth, south-western Australia utilising the framework to enhance the understandings and effectiveness of invasive species management during restoration.

Case study: Utilising the Framework in Restoration Projects in the Canning River, Perth Western Australia

The Swan River estuary flows through the city of Perth, in the south west biodiversity hot spot of Western Australia (Myers et al. 2000). The Swan River and a major tributary the Canning River were identified by the Australian Government's Coastal Catchment Initiative as areas of very high nutrient levels, requiring action to reduce nutrient levels entering the Swan Canning river system. A suite of 11 restoration projects focused on the conversion of existing heavily invaded urban drainage lines into "Living streams" resulted (SERCUL 2010), utilizing a number of restoration methods such as: retrofitting existing local drainage systems, restoring natural drainage features removing extensive invasions of multiple invasive alien species, and utilising indigenous vegetation to restore natural habitats and improve visual amenity for the residents (Department of Water 2009). A local, community run coordinating body with extensive restoration experience, SERCUL (South East Regional Centre for Urban Landcare), is responsible for the coordination and the collaborative stimulus for the 10 Project Partners delivering the management, implementation and monitoring phases for these 11 restoration projects. A workshop (facilitated by Author 2, JF) was conducted with SERCUL staff to identify existing knowledge gaps, which if incorporated into restoration projects, had the potential to enhance the effectiveness of restoration in these highly disturbed and invaded ecosystems (Fisher 2011). Critical knowledge gaps identified were: 1. the need to gain a greater understanding of the interactions between native and introduced spe-
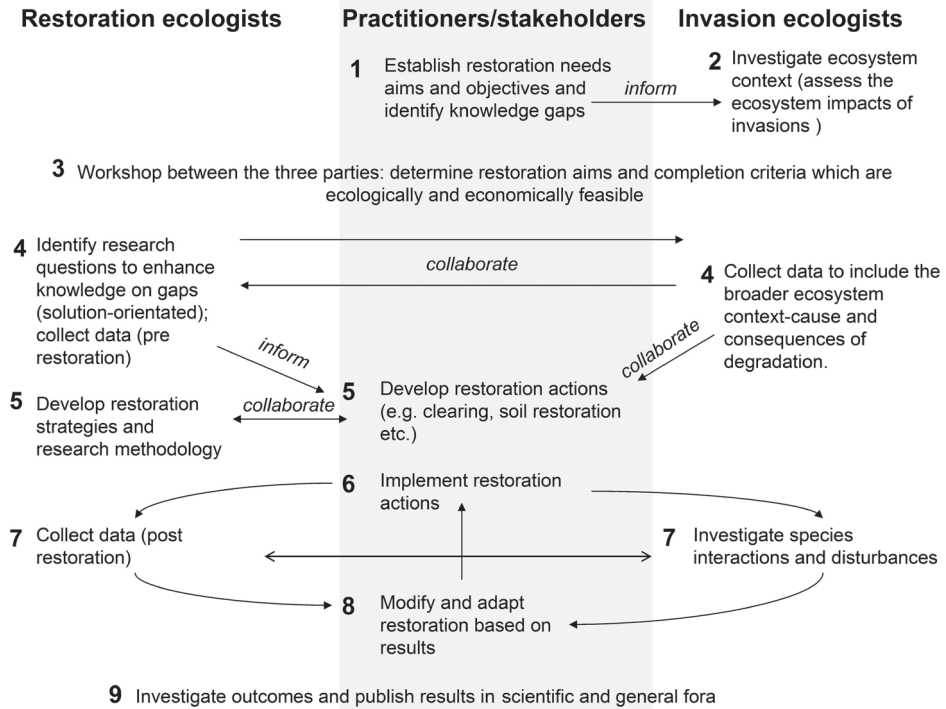
Figure 3. Framework for restoration of sites following alien invasion incorporating practitioners/stakeholders, restoration ecologists and invasion ecologists. Step 1: Practitioners approach restoration ecologist and invasion ecologists with a specific need and aims for ecosystem restoration and an understanding of knowledge gaps. Step 2: Before restoration aims and objectives can be finalised invasion and restoration ecologists assess the impacts of disturbance and invasion on the ecosystem. Step 3: Workshop with restoration and invasion ecologists and practitioners/stakeholders to determine restoration aims and completion criteria which are both ecologically and economically feasible. Depending on the degree of degradation, restoration goals will range from re-establishing a natural ecosystem state, focusing on biodiversity components and ecosystem function, to "only" restoring ecosystem processes and functions. Step 4: Once restoration aims have been identified restoration ecologists identify research questions to enhance knowledge gaps (e.g. how can native species be re-established, how can elevated soil nutrient levels be reduced) with invasion ecologists investigating the broader ecosystem context (e.g. is the invader the cause for ecosystem degradation or are there other underlying causes (e.g. anthropogenic disturbances). Step 5: In a collaborative effort restoration ecologists and practitioners develop restoration actions and research methodology. Before, during and after implementation of the restoration actions, restoration and invasion ecologists collect data to monitor restoration success and investigate species interactions and disturbances. Steps 6–8: Communicate findings to practitioners and modify and adapt restoration accordingly. The iterative feedback of research results into practice guarantees ongoing monitoring and improvement of practice. Step 9: Last, but not least, restoration and invasion ecologists investigate restoration outcomes and publish the results to make the findings available to the scientific and wider community.

cies, terrestrial and aquatic, both before and after restoration actions and 2. the lack of a measured range of ecological indicators which would identify ecosystem restoration trajectories and success. To this end SERCUL, restoration ecologists and practitioners, developed and implemented the framework recommended in this paper (Figure 3), and utilised restoration and invasion ecologists' (Author 2, JF) expertise in the early project development phases and ongoing analysis and interpretation phases of the 11 restoration projects (Figure 3, Steps 1,2,3, 7 and 8). The identified knowledge gaps have been utilized to develop research, monitoring and evaluation programs, including an integrated ecosystem assessment to provide greater understandings of the outcomes of the restoration projects (Fisher 2011). Following the identification of these key knowledge gaps, (Figure 3, Step 1) objectives were defined and baseline data collection criteria developed and implemented, based on the restoration and invasion ecologists' input (Figure 3, Steps 1, 2, 3 and 4). The outcome has been the development of a rigorous and scientifically valid monitoring and evaluation program (publications in preparation) (Figure 3, Steps 5, 6, 7), with opportunities and scope to adapt restoration actions (Figure 3, Step 8). The collaborative approach has resulted in an extensive accumulation of knowledge from numerous, often untapped sources, which have then been incorporated into the design and implementation of all projects. The benefits of collaborative outcomes have been cost and time reductions, a bridging of the knowing-doing gap (Esler et al. 2010), restoration methods determined in an informed and agreed manner incorporating both the doer and the long term manager, expansion of knowledge across all stakeholders with an inherent acquisition of knowledge incorporated into normal practice.

During the implementation of the framework SERCUL identified, as a high priority, the need to develop an enhanced knowledge base with a greater understanding of the ecosystem mechanisms which influence restoration pathways. The gathering of such data provides the added advantage of being able to assign a high level of causal inference between the restoration actions and the ecosystems' response to these actions (Figure 3, Steps 6, 7, 8) (Cottingham et al. 2005). The collaborations forged during the implementation of the framework have led to the incorporation of expanded monitoring and research strategies and methodologies, including measurements of the diversity of ecosystem components and interactions to better understand the implications of restoration actions on ecosystem processes and function. The restoration practitioners are now able to provide, in line with their long term aims, effective evaluation of projects, and credible guidance for future restoration projects and ecological understandings of the newly developed "Living Streams", while obtaining a greater understanding of the processes and functioning of the pre and post restored ecosystems (Figure 3, Step 9) (Clark et al. 2011). The extensive collaboration which has occurred as part of this project and the practitioners' needs to understand more about the ecosystem effects of their restoration actions has changed numerous stakeholders methods and understandings and the on going manner in which assessment and measurement of the effectiveness of nutrient intervention and invasive species management programmes are conducted.

Conclusion

While a link between the disciplines of invasion and restoration ecology exists in the scientific literature, there is still room for improvement with the aim of strengthening the practical outcomes of both fields. Specifically, invasive species, the ecosystem context and the feedbacks between the two are important considerations to include into restoration planning and goal setting. Understanding the consequences of restoration actions provides a mechanism to more rapidly respond to and adapt management actions to build resilient ecosystems. A combined effort from both disciplines with a focus on understanding the interactions of species, both native and non-native, could greatly improve our understanding of ecosystem shifts thus potentially providing new and different solutions to more effectively protect biodiversity and manage alien species during restoration actions.

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Appendix S1

Key journals used for a literature review on linkage between the disciplines invasion biology and restoration ecology. Selection of key journals followed Pyšek et al. (2006)

Key journals invasion biology	Publisher	Scope of Journal (relevant to our study)
Applied Vegetation Science	Wiley Blackwell, International Association for Vegetation Science	Any community-level topic relevant to human impact on vegetation, including amongst others restoration of plant communities.
Austral Ecology	Wiley-Blackwell, The Ecological Society of Australia	Experimental, observational or theoretical studies on terrestrial, systems.
Biodiversity and Conservation	Springer	Articles on all aspects of biological diversity - its description, analysis and conservation, and its controlled rational use by humankind.
Biological Invasions	Springer	Patterns and processes of biological invasions in terrestrial ecosystems. Management and policy issues related to conservation programs and the global amelioration or control of invasions.
Diversity and Distributions	Wiley-Blackwell	Application of biogeographical principles, theories, and analyses to problems concerning the conservation of biodiversity including the study of biological invasions.
Ecology	Ecological Society of America (ESA)	All aspects of ecology.
Ecological Applications	Ecological Society of America (ESA)	Integration of ecological science and concepts with their application and implications. Papers that develop the basic scientific principles on which environmental decision-making should rest, and those that discuss the application of ecological concepts to environmental problem solving, policy, and management.

Key journals invasion biology	Publisher	Scope of Journal (relevant to our study)
Ecological Monographs	Ecological Society of America (ESA)	Empirical and theoretical advances in the field of ecology.
Ecosystems	Springer	Ecosystems services and management.
Journal of Ecology	British Ecological Society	All aspects of the ecology of plants in terrestrial ecosystems.
Journal of Vegetation Science	Wiley Blackwell, International Association for Vegetation Science	Methodological and theoretical studies, and descriptive and experimental studies of plant communities and plant populations.
Oecologia	Springer	Conservation Ecology
OIKOS	Wiley Blackwell, Nordic Society OIKOS	Aspects of ecology, defined as organism-environment interactions.
Plant Ecology	Springer	Findings of pure and applied research into the ecology of vascular plants in terrestrial and wetland ecosystems.
Wetlands	Springer	All aspects of wetlands biology, ecology, hydrology, water chemistry, soil and sediment characteristics, management, and laws and regulations.

Appendix S2

Types of restoration as defined by the main aim of the study

Types of restoration	Examples
Restoration after anthropogenic disturbances	Restoration of old fields, restoration after mining
Wetland restoration	Restoration of riparian ecosystems and wetlands, restoration of water bodies
Erosion control	Restoration of road sides
Forest restoration	Restoration of degraded forest or re-establishment of secondary forests
Grassland restoration	Restoration of grasslands after agricultural use
Restoration after alien invasion	Studies with an explicit focus on the control of invasive alien species
Restoration of arid lands	Restoration of degraded rangelands, dune restoration and savanna restoration
Shrubland restoration	Restoration of shrublands after degradation
Soil restoration	Restoration of soils after contamination or agricultural use
Species restoration	Re-introduction of specific (endangered) species

Appendix S3

Variables and categories used for analysing the linkage between Restoration Ecology and Invasion Biology (methodology follows Aronson et al. 2010).

Category	Key words and Definitions
Study objective	Is invasion control the explicit aim?
Country	Country where restoration/alien invasion took place
Ecosystem in which the study was conducted	Grassland, forest, wood and savanna, shrubland, arid and semi-desert and desert, rivers, other wetlands, marine and costal, urban, human modified and transformed, other or unclassified
Causes of degradation (according to UNEP 2003, modified)	Deforestation Overgrazing Agricultural activities (other than grazing) Overexploitation of vegetation (e.g. fuel wood consumption) Industrial activities (Alien) invasion (includes native invasions)
Causes of degradation (invader)	Replacing/outcompeting native plants Decline of native species richness Changes in native species composition/structure Changes in soil properties (e.g. nutrient enrichment) Changes in native soil seed bank (depletion) Change of disturbance regimes (e.g. fire regime) Others (e.g. impact on native fauna)
Invasion control	Biological control Mechanical control Herbicide control Alteration of soil nutrients Follow-up control Burning
Restoration approach; measures implemented beyond removal of invader	Sowing or planting Soil improvement (i.e. mulching, ploughing, top soil removal) Change of grazing regime Manipulation of hydrological regime Removal of competitive neighbour plants Solarisation
Reasons for additional measures	Lack of native species establishment / depleted native seed bank Competitive advantage of invader Prevent alien species spread/reduce susceptibility to invasion System resistant to restoration/break positive feedback loop (e.g. changes in fire regime) Highly degraded site (e.g. after agricultural use) Nutrient enriched soils Not specified