

Abundance, rarity and invasion debt among exotic species in a patchy ecosystem

Joseph R. Bennett · Mark Vellend ·
Patrick L. Lilley · William K. Cornwell ·
Peter Arcese

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Abstract Community assembly through species invasions is a long-term process, for which vital information regarding future trends can be contained in current patterns. Using comparative analyses of native and exotic plant assemblages from meadow patches on islands in British Columbia, Canada, we examined multiple lines of evidence for ‘invasion debt’, a latent expansion of exotic species populations.

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J. R. Bennett · P. Arcese
Centre for Applied Conservation Research, University of British Columbia, 2424 Main Mall, Vancouver, BC V6T 1Z4, Canada

J. R. Bennett (✉)
Environmental Decisions Group, University of Queensland, Brisbane, QLD 4072, Australia
e-mail: j.bennett5@uq.edu.au

M. Vellend
Département de biologie, Université de Sherbrooke, Sherbrooke, QC J1K 2R1, Canada

P. L. Lilley
A Rocha Canada, 19353 16th Ave, Surrey, BC V6J 1H3, Canada

W. K. Cornwell
Faculty of Earth and Life Sciences, Vrije Universiteit Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands

We show that: (1) short-dispersing species are under-represented compared to their long-dispersing counterparts in exotic species only; (2) among species that are invasive elsewhere in North America, a greater proportion of long dispersers are common in the study area and a greater proportion of short dispersers are rare; and (3) time since arrival in the study region is positively related to number of occurrences in exotic species. In addition, we show that a suite of exotic species possesses the facility of rapid long-distance dispersal and ability to establish viable populations on even the most isolated and least disturbed patches. While some highly-dispersive exotic species can rapidly colonize new areas, short dispersers appear to exhibit invasion debt, with their potential distributions only being realized in the long term. Removing or even reducing populations of many rapid colonizers could be extremely difficult; however, for species exhibiting patterns most consistent with invasion debt, an opportunity exists for monitoring and removal to help reduce potential competition with native species.

Keywords Dispersal ability · Invasion debt · Forms of rarity · Garry oak ecosystem · Invasive species · Super-invaders

Introduction

Predicting the impact of invasive exotic species has become an important goal of ecological research.

Species invasions also provide ecologists with opportunities to witness community assembly at easily observable temporal and geographic scales, facilitating tests of ecological theory (Daleo et al. 2009). A common approach to understanding species invasions is to identify characteristics that differentiate invasive exotic species from native or non-invasive exotic species, and then to infer that these distinguishing qualities are predictors of invasiveness. Results of such studies have been mixed, with several analyses revealing characteristics linked to invasiveness (e.g. Callaway and Aschehoug 2000; van Kleunen et al. 2010), while others indicate that the characteristics of native and invasive species largely overlap (e.g. Daehler 2003; Leishman et al. 2010), or that changes in externalities such as resource availability (Davis et al. 2000) and disturbance (MacDougall and Turkington 2005; Vilà et al. 2007), rather than species characteristics, are the main drivers of invasion.

Much of the discrepancy in such comparisons may be due to the focus of most analyses on a single geographic scale (Shea and Chesson 2002; Strayer et al. 2006) and on currently dominant species, while neglecting potential indications of long-term change via species that have yet to reach their potential distributions. Recent colonists or species that lack the capacity for long-distance dispersal may not appear to be invasive when in fact they are in the process of initial range or population expansion (Strayer et al. 2006). Indeed, latent range expansions potentially exist for many exotic species that are currently uncommon, representing an ‘invasion debt’ (sensu Seabloom et al. 2006; Essl et al. 2011). Thus, it is important to determine what the current patterns among native and exotic species can tell us about long-term trends.

Here, we test for patterns in native and exotic species occurrences at different scales that are predicted by an invasion debt hypothesis, in vascular plant communities from 67 discrete meadow patches located on Vancouver Island, British Columbia, and adjacent smaller islands. We use a multi-faceted approach to determine the statistical relationships between the abundance of species and their origin, dispersal ability and life form, and then use detailed analyses of these patterns to test for indicators of invasion debt in exotic species assemblages. High diversity of both native and exotic species in our study

system, the discreteness of individual patches (including some located on isolated, relatively undisturbed islands), and the comparatively recent history of species introductions, make it ideal for examining the process of species invasion.

An area experiencing invasion debt will display differences in abundance patterns between exotic species and long-term native residents that are reflective of the relatively recent arrival of the exotics. Thus we predicted the following: (1) Exotic short-dispersing species would be underrepresented compared to other species, because they have not had sufficient time to disperse to all suitable habitat; (2) frequencies of exotic species in general would be related to time since arrival in the region; (3) among exotic species identified as being invasive elsewhere in North America, a smaller proportion of short dispersers than long dispersers would be common in the study area (and a greater proportion would be rare); and (4) exotic species of all types would be underrepresented on small, isolated island patches, reflecting the relative inaccessibility of the most isolated patches, the recent arrival of exotic species in the study region, and the possible role of disturbance agents in aiding propagule spread of exotic species (cf. MacDougall and Turkington 2005). While fulfilment of any one of the predictions above does not allow firm conclusions to be made, fulfilment of all or most of them provides strong weight of evidence for the existence of invasion debt.

In contrast to the large scale (e.g. national, province/state) of most analyses of the roles of time and species characteristics in invasion (e.g. Lloret et al. 2004; Seabloom et al. 2006; Williamson et al. 2009; Ahern et al. 2010), we examined patterns of commonness and rarity at two ecologically-distinct spatial scales: first, by surveying the frequency of occurrence of 188 native and 113 exotic species among discrete habitat patches, and second by sampling their occurrence among small plots located within patches. We report multiple lines of evidence supporting the invasion debt hypothesis, strongly suggesting incipient changes in community composition in the study area. We also demonstrate the existence of a suite of exotic species that appear to possess the ability to rapidly colonize even the most isolated and least disturbed sites in the study area.

Methods

Study area

Our study sites were comprised of discrete lowland meadow patches located in the Southeast rainshadow of Vancouver Island, British Columbia, and adjacent smaller islands in the Strait of Georgia. The climate in the study area is sub-Mediterranean, with cool, wet winters and frequent summer drought (MacDougall 2005). The meadow patches in the study area are collectively referred to as the Garry oak ecosystem, due to the common occurrence of Garry oak (*Quercus garryana*) trees within them. Palynological evidence indicates that these meadows may have been present on and near Vancouver Island since shortly after deglaciation (~11,000 a BP), and reached their maximum extent during the Hypsithermal period (~8,500–6,000 a BP; Pellatt et al. 2001). After this time, the meadows may have diminished in extent, but were likely maintained to a large degree by deliberate landscape manipulation by Aboriginal people using fire, especially in areas of deeper soil that otherwise tend to revert to Douglas-fir woodland (MacDougall et al. 2004). Subsequent European colonization led to the cessation of Aboriginal land management practices and loss of ~90 % meadow habitat, through direct conversion to farmland as well as forest encroachment (Bjorkman and Vellend 2010). Presently, meadow patches tend to be located on shallow-soil areas isolated from one another by forest, ocean and/or human development. They are considered to be floristically diverse, and a high priority for conservation (Fuchs 2001), but are also highly invaded by many exotic plant species. In some areas, exotic species occupy most of the ground cover, and are thought to threaten populations of native species (Fuchs 2001). Various factors have been proposed as causes of exotic species abundance in the study system, including altered fire regimes (MacDougall 2005), human disturbance (Lilley and Vellend 2009), increased herbivory of native plants (Gonzales and Arcese 2008), and propagule pressure from neighbouring farms and roadsides (MacDougall and Turkington 2005). Our sites were chosen from among the best-preserved examples of these meadow patches, within a representative range of their current distribution in Canada.

Community surveys

In 2006, 2007 and 2008, 67 meadow patches on Vancouver Island and the southern Gulf Islands of British Columbia, ranging in size from ~0.2 to 17.7 ha, were surveyed for vascular plants (see Supplementary Material 1 for details). Surveys took place from April to June, when most plants in the study system are easiest to identify. In patch-level surveys, the patches were systematically surveyed across their full extents. For quadrat-based, intra-patch surveys, we used a stratified-random selection of quadrats (described in Supplementary Material 1). The number of quadrats per patch ranged from 5 to 15, depending on patch size. This allowed us to approximate within-patch species frequencies across the total area of suitable habitat in the study sites. A total of 484 1-m² quadrats were surveyed. Plants were identified to the species level or lower in 95 % of cases, using the nomenclature scheme of Douglas et al. (1998–2002). Those taxa that could not be identified to species level or lower were combined in the cases of taxa of the same genus that were near-identical in appearance and habitat (e.g. *Luzula comosa/multiflorum*), and were otherwise excluded from analyses.

Species characteristics

The presence or absence of widely-recognised dispersal-aiding adaptations (e.g. hooked awns, pappus, edible fruit, adhesive seeds) was used as a proxy for dispersal ability, which was treated as a binary variable (“short” vs. “long” dispersers). For all species not possessing obvious characteristics facilitating long-distance dispersal, the primary literature was searched for evidence of long-distance dispersal capacity (e.g. consumption by animals and survival in their guts). Fifty-two of 353 species that could not be unambiguously categorised were eliminated from analysis, resulting in a pool of 301 species classified by origin, dispersal ability and life form (Table 1). These classifications were the predictor variables in the generalised linear model (GLM) framework described below, with the number of occurrences of a species across either patches or quadrats being the response variable.

Table 1 Number of species according origin/dispersal and life form category

	Native	Exotic
Short dispersers		
Forb	81	40
Graminoid	3	0
Shrub	1	1
Tree	0	1
Long dispersers		
Forb	52	40
Graminoid	15	22
Shrub	22	8
Tree	14	1

Rarity and commonness at combined scales

The relative abundances of species do not necessarily translate across scales: some species may be common at one scale and rare at another (Rabinowitz 1981). Therefore, to simultaneously compare abundances at both the inter- and intra-patch scales, we used a modified version of Rabinowitz's "Forms of Rarity" framework (Rabinowitz 1981), which permitted analysis of factors associated with commonness and rarity at both the inter- and intra-patch scales together, as well as focused examination of the factors associated with extremities of distribution patterns ('common', 'rare'). In her original framework, Rabinowitz (1981) included seven forms of rarity and one form of commonness, based on local abundance, regional distribution and environmental specialisation. Since environmental specialisation could not have been reasonably determined for rare species in the dataset (due to too few occurrences) and thus the environmental specialisation component of the Rabinowitz framework could not be reliably determined for such species, we limited our characterisations to the following: rarity at both inter- and intra-patch scales; rarity at the intra-patch scale but commonness at the inter-patch scale; rarity at the inter-patch scale but commonness at the intra-patch scale; and commonness at both scales. For the inter-patch scale, we defined 'common' as presence in at least 15 patches, and 'rare' as presence in two or fewer patches. For the intra-patch scale, 'common' was defined as presence in two or more quadrats in at least one patch, and 'rare' as presence in one or fewer quadrats in any patch. Note

that 149 of 301 species were found in patch-level surveys but not in any quadrats. Since our definitions of commonness and rarity were necessarily arbitrary, we conducted analyses on more liberal or conservative classification schemes. These yielded similar results (see Supplementary Material 5).

Time since arrival and invasiveness in other regions

To estimate time since arrival for exotic species, records from the two largest herbaria in the Pacific Northwest of North America, at the Universities of Washington and British Columbia, were searched for the year of the earliest naturalised specimen (i.e., outside of human cultivation according to voucher labels) in the region (defined as the Coast Mountains westward, within Washington State and British Columbia). Collections at the UBC Herbarium were hand-searched, as the online records were incomplete at the time of writing. Even in a well-collected locale such as the study area, estimates of arrival time based on herbarium specimens represent minima, as time elapses between establishment and collection. The earliest date from either herbarium record was used to minimise the potential for lag times to bias results. To determine the proportions of exotic short and long dispersers known to be invasive elsewhere and common or rare in our study area, we examined the North American database of invasive species (invasive.org) to identify species independently classified as 'invasive' by provincial or state management agencies elsewhere in North America.

Patterns on isolated/least-disturbed patches

To determine whether invasion debt is indicated by underrepresentation of all exotic species on the isolated and least-disturbed patches, a subset 22 patches located on small islands in the study area was analysed separately. All 22 patches are under federal or provincial protection, or are in the legislative process of becoming protected, due to their relatively pristine condition and conservation value, and they have no history of agricultural use (e.g. grazing), nor current evidence of trails. Within 1,000 m buffers around these patches, the mean area of agricultural land and length of roads were each ~100 times less than for the Vancouver Island

patches (J. Bennett, unpublished data). While the effects of isolation and low disturbance cannot be separated for these islands, both their relative isolation and low disturbance were predicted to decrease the representation of exotic species of all types.

Statistical analyses

Tests for species' attributes associated with differences in number of occurrences or rarity/commonness designation were conducted in a GLM framework. All species were considered in each model, with the response variable being the number of occurrences of every species, and origin, dispersal ability and life form being the categorical predictor variables. This framework allowed us to test for differences in abundances among species grouped according to the predictor variables. Nested-subset models were produced using all possible variable combinations, beginning with complex models using all possible interaction terms and proceeding to simple, single-variable models. Models were compared using likelihood ratio tests to determine whether additional variables resulted in significantly greater fit, with the most parsimonious model retained as the best set of predictors for each response variable. We conducted an additional patch-level analysis normalizing for the multiple quadrats surveyed in each patch (see Supplementary Material 4). This analysis used predictor variables as above, and the mean proportion of quadrats occupied per patch for each species as the response variable. This is somewhat different from the intra-patch analyses in that it measures intra-patch level dominance among patches (as opposed to intra-patch level presence among all quadrats).

To explore the role of time since arrival, models were created using exotic species only, and including estimated time since arrival as an additional (continuous) predictor variable. To assess whether time since arrival was related to the spatial extent of exotic species distributions in the study area, additional models were run for exotic species only, with predictor variables as above, and the response variable being range estimates among sample sites using minimum convex polygons of occurrences at the inter-patch scale.

Appropriate error distributions were used for all models. Numbers of occurrences in patches and quadrats were overdispersed counts, so models for

number of occurrences used a negative binomial error distribution (as opposed to quasi-Poisson, which precludes likelihood ratio tests); forms of rarity/commonness models used a binomial distribution. In the most parsimonious models, t-tests of coefficients for individual categories within the categorical variables were used to determine their significance. All statistical analyses were conducted using R v.2.12.0 (R Development Core Team 2010).

Phylogenetic analyses

If phylogenetic relationships among species being compared are themselves related to the response variable of interest, species may demonstrate a lack of independence as data points (cf. Harvey et al. 1995). Phylogenetic relationships may also reveal testable patterns that can allow generation of new hypotheses that could not be derived using species themselves (e.g. Cadotte et al. 2010). We therefore examined the potential influence of phylogeny in our data using two approaches. To determine whether phylogenetic distances were smaller within than among groups selected in the most parsimonious models outlined above, we used permutation tests, randomly rearranging group identities to compare intra-group phylogenetic differences to inter-group differences (see Supplementary Material 2 for details). Next, to determine whether there was a phylogenetic signal related to abundance itself (our response variable in the models above), we generated matrices of abundance differences among species at the inter- and intra-patch scales and tested for a phylogenetic signal in abundance data, using a Mantel test with Spearman rank correlation to compare the phylogenetic and abundance differences. The former analysis indicated slightly lower phylogenetic distances within than outside selected groups, except for native long dispersers (Supplementary Material 2), while the Mantel test indicated a very weak phylogenetic signal in abundance (inter-patch scale: $R^2 = 0.002$, $P = 0.035$; intra-patch scale: $R^2 = 0.004$, $P = 0.045$). Thus, while some groups are comprised of species more closely related than random samples of species, there is a negligible connection between phylogeny and abundances of species themselves. We therefore interpreted the differences in abundance among groups in terms of their ecological traits, rather than their phylogenetic relatedness.

Results

In models testing for correlates of species' abundances at both inter- and intra-patch scales, the model with origin interacting with dispersal ability was most parsimonious (Table 2), and exotic short dispersers were significantly underrepresented at both scales (Fig. 1a, b). In addition, exotic long dispersers were overrepresented at the inter-patch scale (Table 2; Fig. 1a). Results for patch-level analyses using mean proportions of quadrats occupied were similar (Supplementary Material 4). However, in this case, the most parsimonious model included an additional term for life form, along with the interaction between origin and dispersal mechanism as per inter- and intra-patch models above. Graminoids in general (both native and exotic) were overrepresented at this level, and exotic short dispersers were somewhat underrepresented (Supplementary Material 4).

Models of commonness and rarity in our modified Rabinowitz framework followed similar patterns to those of single-scale models. Our classification scheme yielded 203 species which could be categorised by form of commonness or rarity, while the remaining 98 species of intermediate abundance were

not classified. Ninety percent of the 203 classified species were categorised as rare ($n = 90$) or common ($n = 91$) at both inter- and intra-patch scales, and thus either well or poorly represented both within and among patches. In contrast, 20 species were common at the inter-patch scale but rare at the intra-patch scale, and two were rare at the inter-patch scale and common at the intra-patch scale. Sufficient data existed to model the species categories related to commonness at the two scales and rarity at the two scales. In both cases, the model with origin interacting with dispersal ability was most parsimonious. Exotic short dispersers were a significant negative predictor of commonness at both scales combined, while exotic long dispersers were a significant negative predictor of combined-scale rarity (Table 2; Fig. 1c).

Estimated time since arrival was included as a variable in the most parsimonious models for exotic species only at the inter- and intra-patch scales, in addition to dispersal ability, but not the interaction term (Table 2). Using minimum convex polygon range estimates as the response variable also resulted in estimated time since arrival and dispersal ability being retained in the most parsimonious model. Though exotic short dispersers appear to have been

Table 2 Significant coefficients from the most parsimonious models for numbers of occurrences and forms of rarity/commonness

Response variable	Predictor variables	Final model	Coefficient	Coefficient value	Standard error	t	P
Number of occurrences in patches	O, D, G _f	O × D	EL	0.364	0.169	2.16	0.0342
			ES	-0.756	0.192	3.95	0.0003
Number of occurrences in quadrats	O, D, G _f	O × D	ES	-1.109	0.418	2.65	0.0114
Commonness on both inter- and intra-patch scales	O, D, G _f	O × D	ES	-1.626	0.472	3.44	0.0014
Rarity on both inter- and intra-patch scales	O, D, G _f	O × D	EL	-1.008	0.365	2.77	0.0073
Number of occurrences in patches (exotic spp. only; including estim. time since arrival)	D, G _f , T _a	D + T _a	T _a	-0.453	0.103	4.40	<0.0001
Number of occurrences in quadrats (exotic spp. only; including estim. time since arrival)	D, G _f , T _a	D + T _a	T _a	-1.479	0.280	5.28	<0.0001
Minimum convex polygon size (exotic spp. only; including estim. time since arrival)	D, G _f , T _a	D + T _a	T _a	-0.210	0.095	2.22	0.0292
Number of occurrences in patches (22 small-island patches only)	O, D, G _f	O × D	ES	-1.500	0.259	5.798	<0.0001
Number of occurrences in quadrats (22 small-island patches only)	O, D, G _f	O × D	ES	-2.003	0.484	4.135	0.0002

See supplementary material 3 for full results (including non-significant coefficients)

Predictor variables: O = origin (native or exotic); D = dispersal ability (short or long); G_f = growth form (forb, graminoid, shrub, tree); T_a = estimated time since arrival

Predictor variable categories: E = exotic; N = Native; S = short dispersers; L = long dispersers (i.e., EL = coefficient for exotic long dispersers in O × D interaction term)

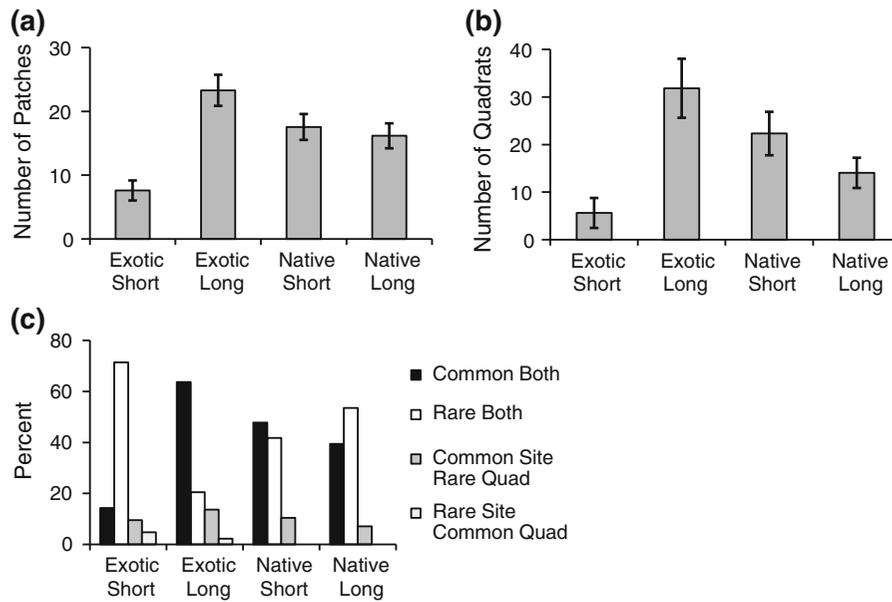


Fig. 1 Frequencies of long- and short-dispersing exotic and native species. **a** Number of patches per species in full patch surveys; **b** number of quadrats per species in quadrat-level

surveys; **c** forms of rarity/commonness per origin/dispersal category. *Error bars* indicate ± 1 standard error

introduced later than exotic long dispersers on average ($t = 4.23$, $DF = 64$, $P < 0.0001$), the independent significant term for arrival time in the model indicates an independent effect of arrival time on abundance and range size of all exotic species. Interestingly, all species present in ≥ 10 quadrats are reported to have been present in the region for ≥ 70 years (Fig. 2).

Comparison with North American provinces and states indicates that exotic short dispersers are currently less often identified as invasive than exotic long dispersers: 22 of 42 (55 %) exotic short dispersers identified in our study area are considered invasive elsewhere in North America, whereas 61 of 71 (86 %) exotic long dispersers are considered invasive elsewhere in North America. However, as predicted, among species that are considered invasive elsewhere in North America, a greater proportion of exotic long dispersers (25 of 61 species) than short dispersers (2 of 22 species) were common at both scales in the study area (Fisher Exact Test, one-tail, $P = 0.028$). In addition, among species that are considered invasive elsewhere in North America, a greater proportion of exotic short dispersers (12 of 22 species) than long dispersers (6 of 61 species) were rare at both scales in the study area (Fisher Exact Test, one-tail, $P = 0.002$).

In the subset of 22 small-island patches, the pattern of representation was very similar to the full dataset (Table 2; Supplementary Material 6). Exotic short dispersers were underrepresented at both scales compared to other species, while exotic long dispersers remained slightly but not significantly overrepresented on a per-species basis.

Discussion

While several previous analyses have clearly shown that incipient invasions exist among exotic species at broad (e.g. national, province/state) scales (e.g. Seabloom et al. 2006; Williamson et al. 2009; Ahern et al. 2010), our analyses utilized smaller, ecologically-distinct scales, and explored the effects of dispersal ability, life form, disturbance/isolation and residence time in species invasions. At both inter- and intra-patch scales, our results support the prediction that exotic short dispersers would be underrepresented, and strongly suggest invasion debt among short-dispersing species at these scales. In contrast, native short dispersers were neither over- nor underrepresented (Fig. 1), and presumably have had time to

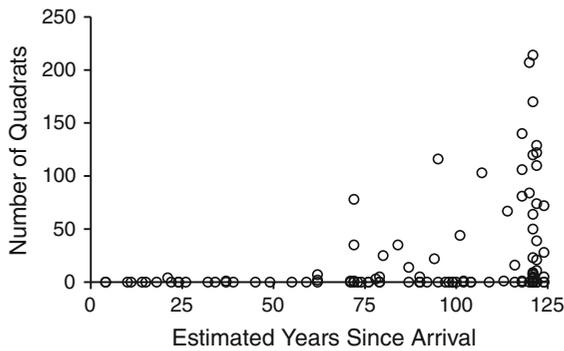


Fig. 2 Number of quadrats in which an exotic species was found versus estimated time since arrival in the region

disperse to much of the suitable habitat in the study area. The importance of arrival time in predicting numbers of occurrences of exotic species at the inter- and intra-patch scales as well as estimated range sizes in the study area, also indicates that invasions in our study area are in an early stage, strongly suggesting invasion debt among the study patches.

While exotic short dispersers appear to be somewhat less invasive as a group than exotic long dispersers based on continent-wide comparisons, among the species that are considered invasive elsewhere in North America, a higher proportion of the short dispersers were rare in our study area. In addition, a higher proportion of the exotic long dispersers that were identified as invasive elsewhere were common in the study area. Both of these patterns suggest that a greater proportion of latent dominant species currently exist among the exotic short dispersers.

The history of species introductions in the study region is relatively short, at <140 years (Reichard and White 2001), compared to >300 years in eastern North America (Mack 2003). In time, some of the exotic short dispersers that have become prevalent in other areas of North America appear likely to become common in the study region, and the relative abundances of long and short dispersers may more closely reflect those of native species, for which long-distance dispersal ability did not significantly relate to abundance. While predicting which exotic short dispersers are most likely to proliferate in our study area in the future is difficult, several species that are currently rare in our surveys are recent arrivals to the region and considered to be invasive in many jurisdictions of North America, including: *Alliaria petiolata* (first

naturalised specimen: 1988); *Allium vineale* (first naturalised specimen: 1961); *Vinca minor* (first naturalised specimen: 1939); and *Hesperis matronalis* (first naturalised specimen: 1937). In addition, there are several exotic short dispersing species that have very close ecological analogues among the native short dispersers that are presently common on drier, shallow-soil microsites. Examples include *A. vineale* versus *Allium cernuum*; *Hyacinthoides hispanica* versus *Camassia* spp.; *Sedum album* versus *Sedum spathulifolium*.

The slight overrepresentation of exotic long dispersers on the 22 relatively isolated and undisturbed island patches did not support our prediction that all exotics would be underrepresented on these sites, as we had expected that even the exotic long dispersers would have had relatively limited opportunity to establish in such places. However, a similar phenomenon was observed by Lloret et al. (2004) at a larger scale on Mediterranean islands, whereby exotic wind-dispersed species were overrepresented compared to other species. While disturbance and human-induced propagule pressure are potential facilitators of the spread of exotic species in our study area (MacDougall and Turkington 2005; Lilley and Vellend 2009), it also appears likely that intrinsic species characteristics such as dispersal ability and pre-adaptation to environmental conditions in the study system have been important in the establishment of exotic long dispersers on even the most isolated and undisturbed patches in our study area.

The fact that exotic long dispersers were less likely to be rare in the combined scales of the Rabinowitz framework than other species, in addition to being overrepresented at the inter-patch scale, is also notable, since the native counterparts to these species have apparently been present in our study area for several thousand years (Pellatt et al. 2001). Indeed, the two most common species at the intra-patch scale, and the first and third most common species at the inter-patch scale (*Aira praecox* and *Hypochaeris radicata*, respectively), are both exotic long dispersers. These findings were unexpected in our study system, because we assumed that the patches and islands represented in our data were substantially isolated from one another by inhospitable dispersal barriers with the potential to delay colonisation. However, several exotic long dispersing species have rapidly overcome these barriers.

The specific life history strategies of some exotic long dispersers may contribute to their invasion

success in our study area, particularly if they are occupying previously-unfilled niches (Emery 2007). However, while alternate forms of rarity and analyses of mean proportions occupied per patch suggested that graminoids in general may be overrepresented versus other life forms, no significant interaction was found between origin and life form in any analysis. Though further research on the detailed morphological and physiological traits of exotic dominants may help to understand the causes of invasiveness, the common exotic long dispersers in this system appear to represent a variety of growth forms and life history strategies that are largely shared with native species. Several of these exotic long dispersers correspond to Daehler's (2003) concept of a 'super-invader', with ability to both disperse to and persist in remote patches. These species do not appear to be dependent on human disturbance for their expansion among and within patches, and appear to be both dispersive and tolerant of environmental conditions in the study system.

While several lines of evidence strongly suggest that an invasion debt exists within our study system, the exact details of future trends are difficult to predict. Our data represent a snapshot in time, so they cannot be used to forecast quantitative trends. However, the results of previous broad-scale studies within countries or provinces/states point to likely directions. Analyses in Europe, where many invasions occurred much earlier than in western North America, have shown that time since arrival is a good predictor of species' range on national scales (e.g. Williamson et al. 2009; Essl et al. 2011). Williamson et al. (2009) suggested that the maximum range within a country of an exotic species may be achieved ~150–300 years after arrival, though infilling within this range would presumably take place over longer time periods. While disturbance may promote range expansion of some exotics, Seabloom et al. (2006) noted that ranges of exotic annual grasses in California are likely expanding ahead of the front of human disturbance. Such a scenario appears to be the case in our study system, despite it being composed of isolated patches, some of which have experienced little direct human impact. Several of the dominant exotic species possess the ability to establish populations throughout the study area, despite seasonal drought that could limit the establishment and persistence of some species (MacDougall 2005). In addition, the

abiotic environment has changed considerably since the first exotic species were introduced in the 1800s, including climate warming (CCCSN 2010) and the fragmentation of Garry oak meadow patches (Lilley and Vellend 2009), both of which will likely continue in future. Since many exotic species in our study system originate in warmer, drier climates (Lilley and Vellend 2009), their invasion may be facilitated by climate change. Thus, even assuming that large areas are protected from human development or 'restored' by management, propagule pressure from already-invaded areas is likely to continue to facilitate the invasion of even the best-conserved sites.

Invasion in our system (and likely others) appears to be a continuous process whereby some highly dispersive species spread rapidly upon arrival, while populations of other species expand more slowly due to lack of long-distance dispersal mechanisms and/or habitat requirements. While newly-arrived species possessing mechanisms for long-distance dispersal should clearly be treated as potential rapid invaders, the exotic short dispersers that possess mechanisms for persistence in Mediterranean climates may be just as important to monitor from management and ecological standpoints. Native species may still outcompete exotic ruderal species in areas requiring specialized adaptations (e.g. shallow-soil, seasonally dry areas; MacDougall and Turkington 2006), and preservation of native diversity in such habitats could be vital to maintaining native biodiversity in this system as a whole. Therefore, removing short-dispersing exotics that possess adaptations to tolerate these conditions may be an important additional management strategy. Proactive removal of species that are known to be invasive elsewhere would also be an efficient management technique. Populations of both of these species groups are generally still low enough in the study system that they can conceivably be controlled or eradicated, without the monumental effort associated with removal of the most common exotic species.

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