RESEARCH ARTICLE



Body size changes in passerine birds introduced to New Zealand from the UK

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Abstract

One feature of global geographic variation in avian body sizes is that they are larger on isolated islands than on continental regions. Therefore, this study aims to assess whether there have been changes in body size following successful establishment for seven passerine bird species (blackbird Turdus merula, song thrush T. philomelos, house sparrow Passer domesticus, chaffinch Fringilla coelebs, greenfinch Chloris chloris, goldfinch Carduelis carduelis, yellowhammer Emberiza citrinella) introduced from the continental islands of the UK to the more isolated oceanic landmass of New Zealand in the middle of the nineteenth century. Measures of tarsus length were taken from individuals from contemporary UK and New Zealand populations of these species, and from historical specimens collected around the time that individuals were translocated from the UK to New Zealand. Analysis of Variance was used to test for size differences between contemporary UK and New Zealand populations, and between historical UK and contemporary UK and New Zealand populations. Historical UK populations have longer tarsi, on average, than 12 (7 UK and 5 New Zealand) of the 14 contemporary populations. Significant decreases in tarsus length relative to the historical populations have occurred in the UK for blackbird, chaffinch and greenfinch, and in the New Zealand blackbird population. Contemporary New Zealand house sparrows have significantly longer tarsi, on average, than both historical and contemporary UK populations. Exposure to novel environments may be expected to lead to changes in the morphology and other traits of exotic species, but changes have also occurred in the native range. In fact, contrary to expectations, the most common differences we found

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were between contemporary and historical UK populations. Consideration of contemporary populations alone would underestimate the true scale of morphological change in these species over time, which may be due to phenotypic plasticity or genetic adaptation to environmental changes experienced by all populations in the last 150 years.

Keywords

Body size, Exotic species, Historical population, New Zealand, Passerine Bird, Tarsus length

Introduction

The traits possessed by species are not fixed, but change in response to a variety of selective forces. The rate of evolution is typically slow (Haldane 1949), meaning that significant trait change is not observed in most species in most human lifetimes. However, more rapid change is possible when species are exposed to new adaptive zones (Futuyma 1979), and so one set of species for which selective forces may change rapidly is those introduced by humans into areas well beyond the limits of their natural geographic distributions. The abiotic and biotic interactions such exotic species experience in their non-native ranges may differ substantially from those in their native ranges (Blackburn et al. 2009, Davis 2009). As a result, we might therefore expect to see relatively fast trait changes in exotic species, through either or both of the processes of genetic adaptation or phenotypic plasticity.

In the second half of the nineteenth century, European colonists introduced more than 100 exotic bird species to the isolated archipelago of New Zealand, as part of organized attempts to naturalise a range of useful and ornamental species there (Thomson 1922, Duncan et al. 2006). Many of these species originated in the European homelands of the colonists (Thomson 1922, Long 1981), and subsequently proceeded to establish viable populations in New Zealand, where they are now widespread and abundant components of the avifauna (Robertson et al. 2007). These species provide a golden opportunity to explore the factors influencing life history trait variation in wild populations, as a series of replicates in a natural experiment on the effects on these characteristics of translocation to a new environment on the opposite side of the planet.

Several studies provide evidence that reproductive life history traits differ between exotic New Zealand populations and native populations of the same bird species in their location of origin. For example, hatching failure rates tend to be higher in New Zealand than in native populations, in inverse proportion to the number of individuals introduced, suggesting an effect of the population bottleneck on this reproductive trait via increased levels of inbreeding (Briskie and Mackintosh 2004). Nine out of eleven species of passerine established in New Zealand following introduction from the UK have significantly smaller clutch sizes, and less seasonal variation in clutch size, in their exotic ranges (Evans et al. 2005; see also Samaš et al. 2013). Eight of these species also show reductions in clutch volume in New Zealand compared to the UK (Cassey et al. 2005). The results for clutch size and its seasonal variation are consistent with Ashmole's hypothesis that variation is driven by the effect of seasonality on resource availability per adult bird (Ashmole 1963), as New Zealand is less seasonal than the UK (Evans et al. 2005), and also match patterns of variation shown by island native bird species relative to their mainland relatives (Covas 2011).

While there is evidence for changes in reproductive traits, to date no study has tested for differences in body size in the native and New Zealand exotic ranges of bird species. Yet, body size is a fundamental characteristic, which tends to correlate strongly with other aspects of a species' life history (Peters 1983). Moreover, there are good grounds to expect that body size will change following introduction to New Zealand.

First, one of the primary features of global geographic variation in avian body sizes is that they are on average larger on islands relative to continental regions, and larger at higher latitudes (Olson et al. 2009). The latitudinal relationship is best explained by variation in temperature and seasonality, through the effects of body size on thermal physiology and starvation tolerance in times of resource scarcity (Olson et al. 2009). Size differences between island and continental birds have been hypothesized to result from differences in thermal physiology (Clegg and Owens 2002, Olson et al. 2009), ecological release from competitors and predators, intensified intraspecific competition, and immigrant selection (Lomolino 2005), although the actual drivers are currently unknown. As New Zealand is one of the most isolated landmasses on Earth, one might expect size increases in species introduced there, especially from continental regions (while UK is also an archipelago, it is barely isolated from continental Europe, and most British bird populations exchange individuals with those on the continent). Conversely, New Zealand lies closer to the Equator than the UK (c. 35-45°S versus c. 50–60°N), and has a more temperate climate on average. If latitude or temperature is the primary driver of size variation, we might expect size decreases in species introduced to New Zealand. However, latitude and insularity might counteract each other and lead to no changes in body size.

Second, the largest members of bird genera are likely to be island taxa more often than expected by chance (Meiri et al. 2011), suggesting again that insularity is accompanied by increase in body size. In fact, recent natural colonists to New Zealand do tend to be smaller than their closest endemic relative, suggesting that isolation on New Zealand is accompanied by increase in body size (Cassey and Blackburn 2004). This effect is more prevalent in smaller birds (taxa <250g): larger-bodied colonists may be larger or smaller than their closest endemic relative with about equal likelihood. However, these size differences may not reflect natural selection within populations as much as different survival, establishment or immigration abilities of species. If so, we may not necessarily see size changes following introduction (but see the next paragraph).

Third, several case studies of recent natural or human-mediated avian colonizations of islands identify differences in body size associated with colonization. For example, Clegg et al. (2002) show that the natural sequential colonization by silvereyes (*Zosterops lateralis*) from Tasmania to South Island, New Zealand (in 1830), and the Chatham Islands (in 1856) has been accompanied by successive increases in size (wing length). Mathys and Lockwood (2009) showed that exotic great kiskadees (*Pitangus* *sulphuratus*) on Bermuda had larger morphological dimensions than individuals from the source population on Trinidad 50 years after introduction. Mathys and Lockwood (2011) also showed that five out of six exotic passerine bird species they examined on the Hawaiian islands showed morphological divergence across islands 80 to 140 years after introduction, although they do not present comparisons with the source population. Amiot et al. (2007) demonstrated morphological divergence within an island by exotic red-whiskered bulbuls (*Pycnonotus jocosus*) over a period of around 30 years. Clines in body size have also been documented for exotic house sparrow and common myna (*Acridotheres tristis*) populations introduced to New Zealand in 1870, with a trend for larger body size in the northern parts of New Zealand (Baker and Moeed 1979, Baker 1980). Similar trends have also been observed in New Zealand exotic mammals (Yom-Tov et al. 1986), and in birds in other parts of the world (e.g. Johnston and Selander 1964, 1971, 1973). All of these patterns of divergence are indicative of changes in body size following establishment.

Here, we test for changes in body size between native and exotic populations for seven species of passerine bird introduced from the UK to New Zealand in the middle of the nineteenth century (Thomson 1922, McDowall 1994). We compare an aseasonal measure of body size - tarsus length - between specimens from present day New Zealand and present day UK, and between individuals from both these populations and individuals collected from the UK in the middle of the nineteenth century. Our expectation is that body sizes should be larger in New Zealand populations than in both historical and contemporary UK populations, based on the generally greater mean body size of island birds (Olson et al. 2009), evidence of size increases in natural avian colonists in New Zealand (Cassey and Blackburn 2004), and previous analyses of bird introductions (Mathys and Lockwood 2009) and invasions to islands (Clegg et al. 2002). As far as we are aware, this is the first time that the body sizes of individuals in exotic bird populations have been compared with individuals in historical source populations, rather than just with individuals in contemporary source populations that may also in theory have undergone morphological changes over the period since the exotic population was introduced.

Methods

We compared contemporary New Zealand (2003 - 2005; N = 140), contemporary UK (2005 - 2011; N = 175) and historical UK (1848 - 1879; N = 126) specimens of blackbird (*Turdus merula*), song thrush (*T. philomelos*), house sparrow (*Passer domesticus*), chaffinch (*Fringilla coelebs*), greenfinch (*Chloris chloris*), goldfinch (*Carduelis carduelis*) and yellowhammer (*Emberiza citrinella*). These species were chosen because specimens were available to us from all three populations of interest. Eight historical specimens of goldfinch (all from 1946), two of greenfinch (both from 1892) and one each of song thrush (1901 and house sparrow (1891) from New Zealand were also available for comparison, although the low sample sizes meant that we only formally

	U	K	New Zealand			
Species	Historical	Contemporary	Historical	Contemporary	Date	
Blackbird	18	16		16	1862	
Song thrush	8	14		15	1865	
House sparrow	25	30		39	1862	
Chaffinch	27	33		4	1862	
Greenfinch	16	28		10	1862	
Goldfinch	11	21	8	4	1862	
Yellowhammer	21	6		23	1862	

Table 1. Sample sizes of tarsus measurements included in the analysis for each population, together with the date of first known introduction into New Zealand from the UK.

analysed these data for goldfinch. These goldfinch specimens date from midway between the date of introduction of this species to New Zealand and the contemporary New Zealand samples, but we may nevertheless predict some change between 1946 and the present. The historical UK specimens bracket the dates of first introduction to New Zealand of all these species (Table 1).

The contemporary New Zealand specimens sampled were all live birds caught opportunistically as part of fieldwork by John Ewen (J.E.) in New Zealand, spanning latitudes from Hauturu to Palmerston North (see Ewen et al. 2012 for a list of sites). The contemporary UK specimens were all frozen samples from the Garden Bird Health initiative (GBHi) archive. These specimens come from across England and Wales, although the majority (approximately two thirds) were from England south of the line connecting the Wash to the Severn Estuary. All were birds found dead by members of the public and submitted to the Institute of Zoology, where biometric measurements were recorded. Post mortem examinations were performed according to a standardised protocol and the carcasses with intact appendicular skeleton were archived at -20°C (Robinson et al., 2010). Carcasses with limb abnormalities or injury were excluded from the study. The specimens were partially defrosted and (with the exception of house sparrow) re-measured by J.E., under an extraction hood in the post-mortem room at the Institute of Zoology, using the same measurement method as for the contemporary New Zealand specimens. The historical specimens (UK and New Zealand) were all skins stored in the bird room of the Natural History Museum at Tring, UK. The majority of UK specimens were again from England south of the line connecting the Wash to the Severn Estuary (around 85%). The specimens were measured by J.E. using the same measurement method as for the contemporary samples.

We used tarsus length as our measure of body size. This is a measure of size that is invariant across seasons and is available for measurement on all the specimens available to us – most other standard aseasonal size measures, such as beak dimensions, wing chord and tail length, were not available on the post-mortemed GBH*i* specimens. Tarsus length was measured as full tarsus using dial Vernier callipers. Measurements were taken twice, with high repeatability: intraclass correlations (Bland and Altman 1996) varied from 0.94 for goldfinch (N = 108, 54 birds) to 0.985 for chaffinch (N = 142, 71 birds). There is some evidence that drying specimens may cause changes to the dimensions of the skins, most often through shrinkage (e.g. Bjordal 1983, Winker 1993, Kuczynski et al. 2002), although dried tarsi may also be longer than when fresh (e.g. Herremans 1985), or show no significant change (e.g. Greenwood 1979). Bjordal's (1983) study is the only one that pertains to a species in our study: he found that house sparrow tarsi shrank by 1.1 - 1.3% on drying. Either way, it should be borne in mind that the historical (museum) specimens measured could differ from contemporary specimens as a consequence of preservation.

All specimens were measured by J.E. except for the contemporary house sparrow specimens from the GBH*i*, for which we used measurements taken by either Becki Lawson (B.L.; N = 28) or Katie Colvile (K.C.; N = 5) during the post-mortem examination. We tested for differences in the measurements made by J.E., B.L. and K.C. using paired t-tests to compare tarsus lengths taken from 25 GBH*i* specimens from 9 different bird species.

For all species except the song thrush, we analysed only birds that had been aged as adult. Birds were classed as juveniles until the post-juvenile body moult was complete. First year birds beyond their post-juvenile moult and adult birds were not differentiated. The tarsus is in any case fully grown at fledging and does not change thereafter, so we do not expect mis-aging of specimens to affect the results. The relative paucity of certain adults in the song thrush samples meant that we combined data from birds of all ages, and tests across all populations confirmed that there was no difference in tarsus length between adults, first years or birds of unknown age (ANOVA: $F_{2,35} = 0.115$, P = 0.89). We also excluded birds of unknown sex for all species except song thrush and goldfinch, for which many specimens could not be unambiguously identified as male or female.

We analysed models of tarsus length that included sex (male/female, or male/female/unknown), population (contemporary New Zealand, contemporary UK, historical UK; and for goldfinch, historical New Zealand), and their interaction, as factors. All analyses were carried out using ANOVA in R v. 2.14.1 (R Development Core Team 2006), with post-hoc comparisons between population means using Tukey's Honestly Significant Difference test. Regressions of tarsus length versus time with sex and location as factors cannot be applied in this case because there is only a single historical population for comparison. Sample sizes for the different populations for each species are given in Table 1, along with the date of first known introduction into New Zealand from the UK as recorded by Thomson (1922). We calculated the rate of change in a population in Darwins as $ln(T2) - ln(T1)/\Delta t$, where T2 equals contemporary tarsus length, T1 equals historical tarsus length, and Δt equals the time difference between the two populations in millions of years.

Results

Means and variances of tarsus lengths for each population of each species are given in Table 2. Full models for tarsus length as a function of population, sex, and their

Table 2. Mean and variance (mm) of tarsus length for each population of each species. % quantifies the change in each contemporary population relative to the UK historical mean, and equals 100 x (contemporary mean/UK historical mean). No measurements are available for historical New Zealand populations of blackbird, chaffinch and yellowhammer, and only single measurements for song thrush and house sparrow. Sample sizes are as in Table 1. The largest population mean for each species is given in bold, and the smallest in italics.

		UK	New Zealand			
Species	Historical	Contemporary	%	Historical	Contemporary	%
Blackbird	39.43 ± 1.66	38.27 ± 0.87	97.1		38.40 ± 0.99	97.3
Song thrush	37.22 ± 1.97	37.10 ± 0.85	99.6		36.25 ± 1.33	97.3
House sparrow	22.34 ± 1.39	21.72 ± 0.96	97.2		23.07 ± 0.26	103.3
Chaffinch	21.93 ± 0.71	20.73 ± 0.42	94.5		21.51 ± 0.55	98.1
Greenfinch	21.72 ± 1.11	21.02 ± 0.40	96.8		21.33 ± 0.33	98.2
Goldfinch	17.72 ± 0.92	17.12 ± 0.22	96.6	17.81 ± 3.14	17.56 ± 0.25	99.1
Yellowhammer	22.80 ± 0.40	21.93 ± 0.64	96.2		22.92 ± 0.68	100.5

Table 3. Results of ANOVA with tarsus length (mm) as the response variable and population, sex and their interaction, as predictor variables. d.f. = degrees of freedom for the comparison.

	Population		S	ex	Interaction	
	F	d.f.	F	d.f.	F	d.f.
Blackbird	7.82***	2,59	1.24	1,59	0.69	2,59
Song thrush	1.67	2,30	1.73	2,30	0.31	2,30
House sparrow	20.05***	2,88	0.03	1,88	1.59	2,88
Chaffinch	17.12***	2,58	11.21***	1,58	0.50	2,58
Greenfinch	4.04*	2,48	0.83	1,48	0.98	2,48
Goldfinch	1.19	3,32	1.90	2,32	0.42	6,32
Yellowhammer	4.46*	2,44	0.83	1,44	3.25*	2,44

* P < 0.05; **P < 0.01; ***P < 0.001

interaction, are given in Table 3 for all species. Sex was a significant predictor of tarsus length only for chaffinch, while the interaction between sex and location was significant only for yellowhammer. Population was a significant predictor of tarsus length for all species except song thrush and goldfinch. Figure 1 shows the median and variation in tarsus length across the various populations for each species, with sexes plotted separately for chaffinch and yellowhammer.

Contemporary UK populations have the shortest mean tarsus length for every species except the song thrush, for which the contemporary New Zealand populations are the smallest (Table 2). Birds from historical UK populations have the longest tarsus lengths for blackbird, song thrush, greenfinch, and chaffinch. Birds from contemporary New Zealand populations have the longest tarsus lengths for house sparrow and yellowhammer, while the longest goldfinch tarsi, on average, are possessed by historical New Zealand birds (Table 2). Contemporary means vary between 94.5% (UK chaffinch) and 103.3% (New Zealand house sparrow) of the UK historical means



NZ C. F. UK H. F. UK C. F. NZ C. M. UK H. M. UK C. M.

Figure 1. Box plots showing the median (dark line), quartiles (box), and range (whiskers) in tarsus length across the various populations for each species. Sexes are plotted separately for chaffinch and yellowhammer, as the models in Table 3 suggest sex differences for these species. NZ = New Zealand; Contemp. and C = contemporary; Hist. and H = historical; F = female; M = male.

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for the species (Table 2). The average change in tarsus length between historical and contemporary means is 2.56%. The maximum absolute change in mean tarsus length is 1.2mm for the UK population of the chaffinch. This equates to a change of around 0.009 mm yr⁻¹ given that the mean sample year was 1871 for historical specimens and 2006 for contemporary specimens, or -416 Darwins.

Post-hoc comparisons on the models plotted in Figure 1 reveal no significant differences between any of the populations for song thrush or goldfinch. For blackbird, birds from the historical UK population have longer tarsi than both contemporary UK (difference \pm 95% confidence interval = 1.16 \pm 0.91 mm, P = 0.009) and contemporary New Zealand (difference = 1.03 ± 0.91 mm, P = 0.023) birds. For house sparrow, birds from the contemporary New Zealand population have longer tarsi than both contemporary UK (difference = 1.34 ± 0.51 mm, P < 0.001) and historical UK (difference = 0.73 ± 0.54 mm, P = 0.005) birds. For greenfinch, birds from the historical UK population have longer tarsi than contemporary UK birds (difference = 0.69 ± 0.59 mm, P = 0.018). The same is true for chaffinch for both male (difference = 1.09 ± 0.75 mm, P < 0.001) and female (difference = 1.18 ± 0.88 mm, P = 0.002) birds. For yellowhammers, contemporary UK females are smaller than females from other populations, but the small sample size for this group (N = 2 females) and their unusually small tarsus lengths relative to all other groups (Figure 1) suggest that these results should not be over-interpreted. Significant differences have relatively high statistical power (mean sample size for significant comparisons = 47.2, mean for non-significant comparisons = 30.6; $F_{1,12}$ = 5.37, P = 0.039), but significant results do also have larger size changes than non-significant results (mean absolute percentage change = 3.52% vs 2.02%; F₁₁₂ = 4.94, P = 0.046), suggesting that power is not the only driver of significance.

Comparison of measurements obtained by the three different measurers from common specimens showed no significant differences in the measurements obtained by J.E. and K.C. (t = -1.68, N = 25, P = 0.11). However, estimates obtained by B.L. tended to be larger than those obtained by both J.E. (t = 5.47, N = 25, P < 0.001) and K.C. (t = 4.68, N = 25, P < 0.001).

Discussion

Increasing numbers of studies are providing evidence for morphological differences between introduced exotic and native source populations of species, for taxa as diverse as plants (e.g. Siemann and Rogers 2008), crustaceans (Torchin et al. 2001), reptiles (Losos et al. 1997), birds (Mathys and Lockwood 2009) and mammals (Simberloff et al. 2000). However, with the exception of experimental manipulations (e.g. Losos et al. 1997), previous studies have tested for morphological differences between contemporary exotic and native populations, rather than between contemporary exotic populations and the historical populations from which introduced individuals were taken. Any observed differences could therefore theoretically have arisen as a result of morphological changes in the exotic population, the native population, or both (c.f. Gordon 1986); without historical data, it would be impossible to say which. Our measures of a morphological feature, tarsus length, from contemporary and historical specimens of a range of species introduced from the UK to New Zealand indeed show that changes have occurred not only in the exotic range, but also in the native range. In fact, contrary to expectations, the most common differences we found were between contemporary and historical UK populations. In the absence of historical size data, we would have greatly underestimated the frequency and extent to which morphological change was occurring in these bird populations.

In the 150 years or so since the seven species in our analysis were introduced from the UK to New Zealand, population mean tarsus lengths have changed by between 0.4 and 5.5%, with an average absolute change of 2.56%. Absolute changes have been greater in the UK populations, averaging 3.14% versus 1.97% in the New Zealand populations. The direction of change has been negative in 12 of the 14 populations, including in all seven UK populations. Contemporary UK populations have the shortest tarsi, on average, for six of the seven species measured. Significant decreases in tarsus length have occurred in the UK populations of blackbird, chaffinch and greenfinch, and in the New Zealand blackbird population. Our a priori expectation was for size increases in the New Zealand populations relative to the historical UK populations, but the only change that fitted this expectation, and indeed the only significant increase in size relative to the historical UK population, was for the house sparrow. The rate of change for the largest difference in these data, for the UK population of the chaffinch, is equivalent to -416 Darwins. This is larger than 89% of the rates of morphological change estimated by Millien (2006) for island populations of mammals. We cannot tell from these data whether the difference is the result of genetic adaptation or phenotypic plasticity (see e.g. Merilä 2012), but either way, it represents a relatively rapid size change.

Previous studies that have tested for morphological differences only between contemporary exotic and native populations may also fail to identify instances where morphological changes have occurred over time, if parallel changes occur in both populations. An example is provided in our data by the blackbird. Here, the contemporary UK and New Zealand populations do not differ significantly in tarsus length, but both contemporary populations have significantly shorter tarsi than the historical source population from the UK. Comparison of the contemporary populations would lead to the erroneous conclusion that no morphological change had occurred in the exotic population after introduction. It follows that the absence of any morphological difference between contemporary exotic and native populations does not necessarily mean that no changes have occurred in these populations over the period since the exotic population was introduced. One should not forget that native populations can change too, particularly in response to current human-induced environmental change.

A range of previous studies on body size in island birds led us to predict that species might increase in size following introduction to New Zealand. Islands tend to be home to the largest members of bird genera (Meiri et al. 2011), recent colonists to New Zealand have smaller body sizes than their endemic relatives (Cassey and Blackburn 2004), and at least one recent natural colonist is larger in New Zealand than in its source population (Clegg et al. 2002). However, we do not in general find support for this hypothesis in the species analysed in this study. Only two species show increases in mean tarsus length in New Zealand relative to the historical source population, and only for the house sparrow is this increase significant. In contrast, five of the New Zealand populations show reductions in tarsus length following introduction, although again only one of these is significant (the blackbird). We can think of five explanations for the lack of concordance between these findings and our theoretical expectations.

First, tarsus length may not be a suitable measure of body size change in these populations, either because it does not adequately measure body size, or because it is not the relevant aspect of size. In respect to the adequacy of tarsus as a measure of size, Freeman and Jackson (1990) caution against using single metrics to quantify body size in small birds, but conclude that mass or tarsus length are the best single metrics to use. Conversely, Gosler et al. (1998) conclude that tarsus length is a poor measure of size in passerine birds. However, their reason - that the tarsus is fully grown at fledging and does not change thereafter – is actually an advantage for our analysis, as it means that our results are unlikely to be age-related artefacts. Moreover, their results show that tarsus length is commonly correlated with body mass within species of passerine bird. In respect of selection for changes in tarsus length on islands, a recent study of seven native bird species by Wright and Steadman (2012) showed that tarsi tended to be longer on the small island of Tobago than on larger Trinidad, or on the South American mainland. They attributed this difference to the greater variety of perching and foraging opportunities available on islands with reduced interspecific competition. Nevertheless, size changes in our context may be better assessed in terms of body mass than other measures of size, if different sizes on islands versus mainlands are due to intraspecific competition or thermal ecology (e.g. Clegg and Owens 2002). Body mass comparisons are harder to make accurately than are comparisons of tarsus length, as mass varies with individual condition and with season. In any case, body mass estimates are not available for all of the specimens available in this study, and indeed for none of the historical specimens.

Second, the time available since introduction to New Zealand may have been inadequate for the species concerned to have produced the predicted size changes. This seems unlikely. On the one hand, more than 100 generations have been available for size changes to occur in these species, if selection pressure for larger size exists. This has been enough time to produce geographic clines in body size in several exotic species in New Zealand (e.g. Baker and Moeed 1979, Baker 1980, Yom-Tov et al. 1986; but see Baker 1992) and elsewhere (e.g. Johnston and Selander 1964, 1971, 1973, Amiot et al. 2007). On the other, most of the observed size changes observed in New Zealand are decreases. While most of these changes are not significant, they are nevertheless not consistent with directional selection for larger body size, regardless of the time available for those selection pressures to have acted.

Third, there may in fact be no differences in the novel New Zealand versus the native UK environments that would lead to larger size in the former. This might seem

unlikely, as there is evidence from native species that birds do attain larger size on New Zealand (Cassey and Blackburn 2004), while the archipelago is also home to some notable examples of avian gigantism (e.g. Dinornis spp., Notornis spp., Strigops habroptilus). However, the conditions that lead to large size in the native species may have been altered by environmental changes following human colonization. Hypothesised drivers of size increases in small species, such as passerine birds, on islands include ecological release from competitors and predators, intensified intraspecific competition, and immigrant selection (Lomolino 2005). The fact that humans have introduced many species of small passerine bird and several species of mammalian predator (including brush-tailed possum Trichosurus vulpecula, rats Rattus sp., cats Felis cattus, and stoats Mustela erminea; King 2005), to a system previously free of such species, and have altered the immigration process by conducting these introductions, may therefore have removed exactly the pressures that drove body size changes in the native avifauna. As a result, the environment inhabited by the exotic species in New Zealand may not differ fundamentally from their native environment. If so, this suggests that one way to discriminate between different hypotheses for size increases in small species could be by relating size changes in exotic species to other changes to island environments. For example, if size changes were driven by a lack of predators on islands, we would predict that size changes in exotic prey species should only occur on islands on which exotic predators remain absent.

Fourth, those features of the environment that drove size increases in the native New Zealand avifauna may still apply, but may be being offset by new conditions. An obvious candidate is climate change. Official UK Department of Energy and Climate Change figures show that annual average temperatures in central England have increased by around 0.8-0.9°C in the period since bird species were introduced to New Zealand (http://www.decc.gov.uk/en/content/cms/statistics/climate_stats/data/ data.aspx), with a similar increase in New Zealand over the last 100 years (http:// www.climatechange.govt.nz/science). There is substantial global geographic variation in avian body sizes related to temperature, with species living at high latitudes and in cooler climates (and on islands) being generally larger-bodied than their relatives living at lower latitudes or in warmer climates (Olson et al. 2009). If the relationship were causal, climate warming would be expected to result in concomitant declines in the body size of species occupying an area. In line with this expectation, Yom-Tov (2001) demonstrated that the body sizes (masses and tarsus lengths) of several species of passerine declined in Israel over the second half of the twentieth century, while minimum summer temperatures increased over the same time period. The tendency for small decreases in body size in the introduced species in New Zealand may therefore reflect a trade-off between insularity and climate. Climate change may also explain why all seven UK populations show decreases in body size over time. Of course, this does not explain why size decreases were not ubiquitous: house sparrows tended to increase in size in New Zealand, but were one of the species shown by Yom-Tov (2001) to have decreased in tarsus length in Israel.

Climate is not the only aspect of the environment to have changed over the last 150 years. Agricultural intensification in the UK has led to farm landscapes with fewer areas

of non-crop, and lower densities of weeds and insects (Benton et al. 2002). Populations of farmland birds have suffered declines, including several of the species in our analysis (Gregory et al. 2004), in at least some cases as a result of the impact of declines in food availability on winter survival (Siriwardena et al. 1999). Food availability may also impact upon the body sizes attained by the remaining individuals, and cause the reductions seen here too. This explanation seems unlikely to explain the generally lower tarsus lengths for populations in New Zealand, however. The species analysed here typically attain densities an order of magnitude higher in New Zealand farmland versus farmland in the UK (MacLeod et al. 2009), while some of the New Zealand samples come from island nature reserves, which are not farmed and where pesticides and herbicides are not used.

Finally, the possibility that the differences between populations can be dismissed as methodological biases also needs to be considered. The first point to note here is that the small sample sizes available for some populations mean that observed differences – or lack thereof – should not be over-interpreted. Small sample sizes give less power to detect significant differences if they exist. This suggests if anything that the conclusions we base on our results are likely to be conservative, and yet we still found significant changes in tarsus length in most species. Small sample sizes will only be problematic for our conclusions if they are also biased. However, measurements of tarsus lengths for British populations of these species in the literature show a significant difference between sexes only for chaffinch (Cramp 1988, Cramp and Perrins 1994a, 1994b), which was also the only sex difference recovered in our analyses (Table 3). This suggests that the measurements on which our analyses are based are sufficiently accurate and reliable to be of use.

We can also exclude the possibility that differences between populations arise from effects of different measurers. All specimens were measured by J.E., except for the contemporary house sparrow carcasses, which were mainly measured by B.L. Comparisons between measurers showed that B.L. tended to produce longer tarsus measurements than J.E., yet contemporary UK house sparrow tarsi were shorter, on average, than both the contemporary New Zealand and historical UK tarsi measured by J.E.. The effect of different measurers for house sparrow populations means that the observed difference between contemporary UK and New Zealand populations of this species are likely to be conservative, and suggest also that the reduction in size between historical and contemporary UK populations is likely to be greater than that recorded in Table 2.

Differences between populations could, however, be the result of the different types of specimens measured – live birds versus defrosted carcasses versus dried skins. Drying of specimens can in some cases change tarsus length measurements, albeit that drying does not change tarsus lengths of all species in the same direction (c.f. Greenwood 1979, Bjordal 1983, Herremans 1985). Nevertheless, shrinkage seems to be more prevalent and more likely, and drying has been shown slightly to shrink tarsi for one species in our analysis, the house sparrow. However, dried specimens returned the largest population mean tarsus measurements for five of the seven species, while dried tarsi were larger than defrosted specimens in all seven species measured (Table 2). Freezing can also cause shrinkage in specimens if not done correctly, as freeze-drying can occur. While most of the smallest population mean tarsus lengths relate

to measurements made on defrosted carcasses, we think it unlikely that this is an effect of freeze-drying. All carcasses were stored at -20° C in knotted plastic bags inside sealed ziplock plastic bags, and were clearly moist on defrosting. Overall, the relatively large population mean tarsus measurements obtained from dried specimens, and the relatively small population means from frozen specimens, both seem unlikely to be consequences of these methods of preservation. A further possibility is that the frozen individuals were dead carcasses found by members of the public, and may not be representative samples of the populations concerned if smaller individuals are more likely to be found dead. In fact, any or all of the samples we analyse could be biased in unknown ways by collection methods, but in the absence of any evidence on this score, we assume that the samples are unbiased estimates of population parameters.

Differences between populations could also be a consequence of differences in where individuals were sampled, as there is geographic variation in body size across geographic ranges within bird species (Ashton 2002), including in at least two of the species in our samples (Murphy 1985, Merilä 1997). This is unlikely to drive the differences we observed between contemporary and historical UK populations, however, as the majority of specimens in both samples were from the southern half of the UK, and therefore sample only a small proportion of the total native range of the species analysed. The New Zealand samples are also relatively limited in spatial extent; all derive from the northern half the country (Ewen et al. 2012), from sites spanning around 4° of latitude. These exotic populations derived from releases of birds from the UK (thought most likely to have been captured near the major ports in southern England) undertaken by acclimatisation societies in Auckland and Wellington (Thomson 1922), and size differences must then have developed *in situ*. We cannot see how sample site choice in New Zealand could bias comparisons with UK populations. A bias could occur if birds of a certain size were more likely to survive the journey (e.g. smaller blackbirds and larger house sparrows), but we can provide no evidence either way on this point.

In conclusion, comparison of tarsus lengths in contemporary native UK and exotic New Zealand populations of seven passerine bird species reveals a significant difference in only one species, the house sparrow. However, consideration of contemporary populations alone masks the fact that significant changes in tarsus length have occurred over the last 150 years in five populations of four species, and therefore underestimates the true scale of morphological change in these populations over time. UK populations of blackbird, chaffinch and greenfinch, and the New Zealand population of the blackbird have all significantly decreased in size, while house sparrows in New Zealand have significantly increased. Why these particular populations should show significant changes in size over the last 150 years, while others show no changes, is unclear. There are no obvious features of location, species, life history, or gross ecology that relate to this variation. Thus, it remains of considerable interest to explain why some populations have changed in morphological size (tarsus length), but not others (assuming that there is more than simply idiosyncratic or stochastic change occurring), and in addition, whether these changes are the result of phenotypic plasticity or genetic adaptation.

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References

- Amiot C, Lorvelec O, Mandon-Dalger I, Sardella A, Lequilliec P, Clergeau P (2007) Rapid morphological divergence of introduced Red-whiskered Bulbuls *Pycnonotus jocosus* in contrasting environments. Ibis 149: 482–489. doi: 10.1111/j.1474-919X.2007.00671.x
- Ashmole NP (1963) The regulation of numbers of tropical oceanic birds. Ibis 103b: 458–473. doi: 10.1111/j.1474-919X.1963.tb06766.x
- Ashton KG (2002) Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. Global Ecology and Biogeography 11: 505–523. doi: 10.1046/j.1466-822X.2002.00313.x
- Baker AJ (1980) Morphometric differentiation in New Zealand populations of the house sparrow (*Passer domesticus*). Evolution 34: 638–653. doi: 10.2307/2408018
- Baker AJ, Moeed A (1979) Evolution in the introduced New Zealand population of the common myna. Canadian Journal of Zoology 57: 570–584. doi: 10.1139/z79-067
- Benton TG, Bryant DM, Cole L, Crick HQP (2002) Linking agricultural practice to insect and bird populations: a historical study over three decades. Journal of Applied Ecology 39: 673–687. doi: 10.1046/j.1365-2664.2002.00745.x
- Bjordal H (1983) Effects of deep freezing, freeze-drying and skinning on body dimensions of house sparrows (*Passer domesticus*). Cinclus 6: 105–108.
- Blackburn TM, Lockwood JL, Cassey P (2009) Avian Invasions. The ecology and evolution of exotic birds. Oxford University Press, Oxford.
- Bland JM, Altman DG (1996) Measurement error and correlation coefficients. British Medical Journal 313: 41–42. doi: 10.1136/bmj.313.7048.41
- Briskie JV, Mackintosh M (2004) Hatching failure increases with severity of population bottlenecks in birds. Proceedings of the National Academy of Sciences, USA 101: 558–561. doi: 10.1073/pnas.0305103101

- Cassey P, Blackburn TM (2004) Testing a macro-evolutionary relationship using a Holocene island bird assemblage. Ecography 27: 59–67. doi: 10.1111/j.0906-7590.2004.03585.x
- Cassey, P Blackburn TM, Evans KL (2005) Correlated changes in reproductive effort of exotic passerines. Notornis 52: 243–246.
- Clegg SM, Degnan SM, Kikkawa J, Moritz C, Estoup A, Owens IPF (2002) Genetic consequences of sequential founder events by an island-colonizing bird. Proceedings of the National Academy of Sciences, USA 99: 8127–8132. doi: 10.1073/pnas.102583399
- Clegg SM, Owens IPF (2002) The 'island rule' in birds: medium body size and its ecological explanation. Proceedings of the Royal Society B 269: 1359–1365. doi: 10.1098/ rspb.2002.2024
- Covas R (2011) Evolution of reproductive life histories in island birds worldwide. Proceedings of the Royal Society B, 279, 1531–1537. doi: 10.1098/rspb.2011.1785
- Cramp S (1988) (Ed) Birds of the Western Palaearctic. Volume V. Tyrant flycatchers to thrushes. Oxford University Press, Oxford.
- Cramp S, Perrins CM (1994a) (Eds) Birds of the Western Palaearctic. Volume VIII. Crows to finches. Oxford University Press, Oxford.
- Cramp S, Perrins CM (1994b) (Eds) Birds of the Western Palaearctic. Volume IX. Buntings and New World warblers. Oxford University Press, Oxford.
- Davis MA (2009) Invasion Biology. Oxford University Press, Oxford
- Duncan RP, Blackburn TM, Cassey P (2006) Factors affecting the release, establishment and spread of introduced birds in New Zealand. In: RB Allen, Lee WG (Eds) Biological invasions in New Zealand, Springer, 137–154. doi: 10.1007/3-540-30023-6_9
- Evans KL, Duncan RP, Blackburn TM, Crick HQP (2005) Geographical variation in avian clutch size: testing Ashmole's hypothesis using introductions as a natural experiment. Functional Ecology 19: 616–624. doi: 10.1111/j.1365-2435.2005.01016.x
- Ewen JG, Bensch S, Blackburn TM, Bonneaud C, Brown R, Cassey P, Clarke R, Perez-Tris J (2012) Exotic parasite establishment: The origins and characteristics of an avian malaria community in an isolated island avifauna. Ecology Letters 15: 1112–1119. doi: 10.1111/j.1461-0248.2012.01833.x
- Freeman S, Jackson WM (1990) Univariate metrics are not adequate to measure avian body size. Auk, 107, 69–74.
- Futuyma DJ (1979) Evolutionary Biology. 1st edition. Sinauer Associates, Sunderland, Massachusetts.
- Gordon KR (1986) Insular evolutionary body size trends in *Ursus*. Journal of Mammalogy 67: 395–399. doi: 10.2307/1380895
- Gosler AG, Greenwood JJD, Baker JK, Davidson NC (1998) The field determination of body size and condition in passerines: a report to the British Ringing Committee. Bird Study 45: 92–103. doi: 10.1080/00063659809461082
- Greenwood JG (1979) Post-mortem shrinkage of Dunlin *Calidris alpina* skins. Bulletin of the British Ornithological Club 99: 143–145.
- Gregory RD, Noble DG, Custance J (2004) The state of play of farmland birds: population trends and conservation status of lowland farmland birds in the United Kingdom. Ibis 146 s2: 1–13. doi: 10.1111/j.1474-919X.2004.00358.x

- Haldane JBS (1949) Suggestions as to quantitative measurement of rates of evolution. Evolution 3: 51–56. doi: 10.2307/2405451
- Herremans M (1985) Post-mortem changes in morphology and its relevance to biometrical studies. Bulletin of the British Ornithological Club 105: 89–91.
- IPCC (2007) Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, Pachauri RK, Reisinger A (Eds)] IPCC, Geneva, Switzerland, 104 pp.
- Johnston RF, Selander RK (1964) House sparrows: rapid evolution of races in North America. Science 144: 548–550. doi: 10.1126/science.144.3618.548
- Johnston RF, Selander RK (1971) Evolution in the house sparrow. II. Adaptive differentiation in North American populations. Evolution 25: 1–28. doi: 10.2307/2406496
- Johnston RF, Selander RK (1973) Evolution in the house sparrow. III. Variation in size and sexual dimorphism in Europe and North and South America. American Naturalist 107: 373–390. doi: 10.1086/282841
- King CM (2005) The handbook of New Zealand mammals. Oxford University Press, Oxford.
- Kuczynski L, Tryjanowski P, Antczak M, Skoracki M, Hromada M (2002) Repeatability of measurements and shrinkage after skinning: the case of the Great Grey Shrike *Lanius excubitor*. Bonner zoologische Beiträge 51: 127–130.
- Lomolino MV (2005) Body size evolution in insular vertebrates: generality of the island rule. Journal of Biogeography 32: 1683–1699. doi: 10.1111/j.1365-2699.2005.01314.x
- Long JL (1981) Introduced birds of the world. The worldwide history, distribution and influence of birds introduced to new environments. David & Charles, London.
- Losos JB, Warheitt KI, Schoener TW (1997) Adaptive differentiation following experimental island colonization in *Anolis* lizards. Nature 387: 70–73. doi: 10.1038/387070a0
- MacLeod CJ, Newson SE, Blackwell G, Duncan RP (2009) Enhanced niche opportunities: can they explain the success of New Zealand's introduced bird species? Diversity and Distributions, 15, 41–49. doi: 10.1111/j.1472-4642.2008.00498.x
- McDowall RM (1994) Gamekeepers for the nation: the story of New Zealand's acclimatisation societies 1861–1990. Canterbury University Press, Christchurch, New Zealand.
- Mathys BA, Lockwood JL (2009) Rapid evolution of great kiskadees on Bermuda: an assessment of the ability of the island rule to predict the direction of contemporary evolution in exotic vertebrates. Journal of Biogeography 36: 2204–2211. doi: 10.1111/j.1365-2699.2009.02169.x
- Mathys BA, Lockwood JL (2011) Contemporary morphological diversification of passerine birds introduced to the Hawaiian archipelago. Proceedings of the Royal Society B 278: 2392–2400. doi: 10.1098/rspb.2010.2302
- Meiri S, Raia P, Phillimore AB (2011) Slaying dragons: limited evidence for unusual body size evolution on islands. Journal of Biogeography 38: 89–100. doi: 10.1111/j.1365-2699.2010.02390.x
- Merilä J (1997) Quantitative trait and allozyme divergence in the greenfinch (*Carduelis chloris*, Aves: Fringillidae). Biological Journal of the Linnean Society 61, 243–266.
- Merilä J (2012) Evolution in response to climate change: In pursuit of the missing evidence. BioEssays 34: 811–818. doi: 10.1002/bies.201200054

- Millien V (2006) Morphological evolution is accelerated among island mammals. PLoS Biology 4: e321. doi: 10.1371/journal.pbio.0040321
- Murphy EC (1985) Bergmann's rule, seasonality, and geographic variation in body size of house sparrows. Evolution 39: 1327–1334. doi: 10.2307/2408789
- Olson V, Davies RG, Orme CDL, Thomas GH, Meiri S, Blackburn TM, Gaston KJ, Owens IPF, Bennett PM (2009) Global biogeography and ecology of body size in birds. Ecology Letters 12: 249–259. doi: 10.1111/j.1461-0248.2009.01281.x
- Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge. doi: 10.1017/CBO9780511608551
- R Development Core Team (2006) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Robertson CJR, Hyvonen P, Fraser MJ, Pickard CR (2007) Atlas of bird distribution in New Zealand 1999–2004. The Ornithological Society of New Zealand Inc., Wellington.
- Robinson RA, Lawson B, Toms MP, Peck KM, Kirkwood JK (2010) Emerging infectious disease leads to rapid population declines of common British birds. PLoS ONE 5(8): e12215. doi: 10.1371/journal.pone.0012215
- Samaš P, Grim T, Hauber ME, Cassey P, Weidinger K, Evans KL (2013) Ecological predictors of reduced avian reproductive investment in the southern hemisphere. Ecography 36: in press.
- Siemann E, Rogers WE (2008) Genetic differences in growth of an invasive tree species. Ecology Letters 4: 514–518. doi: 10.1046/j.1461-0248.2001.00274.x
- Simberloff D, Dayan T, Jones C, Ogura G (2000) Character displacement and release in the small Indian mongoose, *Herpestes javanicus*. Ecology 81: 2086–2099.
- Siriwardena GM, Baillie SR, Wilson JD (1999) Temporal variation in the annual survival rates of six granivorous birds with contrasting population trends. Ibis 141: 621–636. doi: 10.1111/j.1474-919X.1999.tb07370.x
- Thomson GM (1922) The naturalisation of plants and animals in New Zealand. Cambridge University Press, Cambridge. doi: 10.5962/bhl.title.28093
- Torchin ME, Lafferty KD, Kuris AM (2001) Release from parasites as natural enemies: increased performance of a globally introduced marine crab. Biological Invasions 3: 333–345. doi: 10.1023/A:1015855019360
- Winker K (1993) Specimen shrinkage in Tennessee warblers and 'Traill's' flycatchers. Journal of Field Ornithology 64: 331–336.
- Wright NA, Steadman DW (2012) Insular avian adaptations on two Neotropical continental islands. Journal of Biogeography 39: 1891–1899. doi: 10.1111/j.1365-2699.2012.02754.x
- Yom-Tov Y (2001) Global warming and body mass decline in Israeli passerine birds. Proceedings of the Royal Society B 268: 947–952. doi: 10.1098/rspb.2001.1592
- Yom-Tov Y, Green WO, Coleman JD (1986) Morphological trends in the common brushtail possum, *Trichosurus vulpecula*, in New Zealand. Journal of Zoology 208: 583–593.
- Yom-Tov Y, Yom-Tov S, Moller H (1999) Competition, coexistence, and adaptation amongst rodent invaders to Pacific and New Zealand islands. Journal of Biogeography 26: 947– 958. doi: 10.1046/j.1365-2699.1999.00338.x

RESEARCH ARTICLE



Horticultural markets promote alien species invasions: an Estonian case study of herbaceous perennials

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Abstract

Gardening is a popular pastime, but commercial horticulture is responsible for the introduction of alien species and contributes to invasions in a variety of ways. Although an extensive international literature is available on plant invasions, it is still important at the national level to examine the influence of local factors. Accordingly, 17 nurseries in Estonia that cultivated and sold perennial alien species were selected, and a list of species and prices was compiled. The relationships between species status, and factors such as their abundance in the wild were examined statistically. A qualitative list of the nationally problematic species among herbaceous perennials was also completed. A total of 880 taxa were recorded, of which 10.3% were native and 89.7% alien. In all, 87.3% of the alien species were still confined to cultivated areas. The ecological and socio-economic characteristics of the taxa were described, and lists of the families of casual, naturalised and invasive aliens were provided. Both native and increasing wild alien species have a very similar profile on the market. Alien species that are less expensive, widely available and have more cultivars per species on the market are also more likely to escape. The invasive status and abundance of escaped aliens in an area increases with residence time. In general, socio-economic factors create new and reflect previous propagule pressures from commercial horticulture, which continuously increase the likelihood of alien species surviving and invading new areas. Our findings suggest that these national socioeconomic market-related factors explain much of the invasiveness of various perennial ornamental species, and therefore regional and national authorities urgently need to regulate and control the ornamental plant trade to diminish the risk of new invasions.

Keywords

Perennial alien species, commercial horticulture, human-mediated propagule pressure, residence time, legislation and regulation

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Introduction

Biological and human-mediated mechanisms in invasions of alien plant species are interdependent, and as a result, it is difficult to predict where and why such invasions will occur. However, most plant naturalisations and invaders nowadays originate from and in the future will derive from deliberate importations (Mack and Erneberg 2002, Kowarik 2003, Mack 2003). Specifically, the study of the economic uses of plant species that are invasive in various parts of the world has established that most plant invaders are ornamentals (Weber 2003). These species have been introduced for horticultural use by nurseries, botanical gardens, and individuals (Reichard and White 2001). Of course, invasive alien species can be introduced unintentionally (Pyšek et al. 2011) or by other deliberate pathways developed by humans, e.g., for forestry and agricultural purposes (Mack and Lonsdale 2001, Starfinger et al. 2003). Nevertheless, the expansion and globalisation of the horticultural trade is widely accepted as a principal reason for the increase in alien species (e.g., Dehnen-Schmutz et al. 2007a, 2007b, 2010, Barbier et al. 2011) and it is also widely recognised that many invasions begin in urban domestic gardens (e.g., Smith et al. 2006, Hanspach et al. 2008). On a general macroeconomic scale, income growth is the primary driver of globalisation and there is a clear association between Gross Domestic Product and the richness of alien floras (Hulme 2009). In addition, when the variations in invasion rates were partitioned according to a range of explanatory variables, it was found that only national wealth and population density were statistically significant (Pyšek et al. 2010). These predictors simply reflect the intensity of human activities, in which the horticultural trade is also a relevant component.

There is now an extensive literature that analyses the reasons why certain species become invasive (e.g., Pyšek and Richardson 2007, Küster et al. 2008, Milbau and Stout 2008). Many papers identify particular traits that cause an ornamental alien species to become invasive. For example, Marco et al. (2010) showed that when an ornamental perennial alien species escapes from cultivation, pre-adaptation to the local environment and its potential for spreading vegetatively play important roles, along with gardening practices. Most authors conclude that successful invasion cannot be explained by a single trait or characteristic, but is determined in combination with climatic and environmental factors, species traits, and human uses (Thuiller et al. 2006, Milbau and Stout 2008, Beans et al. 2012, Richardson and Pyšek 2012). The phrase "human-mediated propagule pressure" is often used to explain processes, where propagule pressure is defined as the frequency with which a species is introduced to a site, combined with the number of individuals in each introduction event (Simberloff 2009; see also arguments in Lockwood et al. 2009). Human-mediation multiplies this process and it is connected both to human population size and density and to economic characteristics (Pyšek et al. 2010, Trueman et al. 2010). Species residence time gives another dimension to the propagule pressure: the longer the species is present in an area, the more propagules are spread and the probability of establishing new populations increases (Rejmánek et al. 2005, Milbau and Stout 2008, Trueman et al. 2010, etc.).

Human-mediated propagule pressure from ornamental horticulture itself plays both a direct and implicit role for species to become naturalised and even invasive. At a local level it is particularly important, because it promotes invasions in variety of ways (see, e.g. Reichard 2011): 1) the introduction and reintroduction of new plants; 2) the selection of species and cultivars for characteristics such as climatic suitability and rapid propagation; and 3) the creation of propagules due to long residence time, the pressure of gardening fashions and the great number of garden centres. In Britain, market presence, prices and dates of introduction are among the socio-economic factors that have influenced invasions (Dehnen-Schmutz et al. 2007a). Pemberton and Liu (2009) have also stressed the importance to successful naturalisation of the number of years a plant was sold. The current naturalisation success of North American woody species in Europe is determined by introduction history and particularly by planting frequency (Bucharova and van Kleunen 2009). Selective introduction and human-mediated selection of ornamental plants with fast and abundant germination might increase the risk of species ultimately becoming invasive (Chrobock et al. 2011). Kowarik (2003) suggested that secondary releases of alien species might mimic demographic and dispersal processes that influence population growth and expansion of range, and provide opportunities to species whose propagules are not able to move naturally over long distances. In addition, cultivation (e.g., protection from predators and parasites, drought, cold) can facilitate naturalisation by protecting alien populations from environmental stochasticity (Mack 2000).

It has previously been shown that in the case of the Estonian Alien Flora (Ööpik et al. 2008), the establishment and naturalisation of alien species in a given area depended on the level and type of human mediation. The majority (74%) of 232 naturalised alien species in Estonia originates from deliberate introductions. Overall, approximately half of the alien flora consists of short-lived species, but only 24% of the naturalised species belong to this group. Moreover, cultivation in a cold temperate region has tended to favour perennial species with propagative advantages for attaining greater abundance and higher invasive status; especially in natural and semi-natural habitats. The pattern of invasive species is more diverse, but among the most problematic species there are also deliberately introduced perennials, which have escaped from cultivation and are now spreading aggressively, forming monocultures, are toxic, and causing other conservation or human health problems. Hence, through selection and cultivation, humans increase propagule pressure, while invasion success also increases with alien species' residence time. Consequently, at a national level in countries such as Estonia, it is necessary to examine the influence of local factors more deeply, so that measures can be taken to reduce the probability of invasions.

In this paper, the following questions are raised in order to examine the situation in Estonia in further detail:

(i) What is the number of herbaceous perennial species offered for sale, both to horticultural professionals and amateurs? What is the composition of these species?

- (ii) Is availability (i.e., lower prices at certain outlets) related to the current status of these species, i.e., the presence of the alien species in the spontaneous flora and/ or their abundance in the wild, and how is this connected to species' residence time in Estonia?
- (iii) Does this list include problematic or even legally prohibited alien species that may cause nature conservation problems and therefore needs national attention?

Material

Background information about Estonia

Estonia lies approximately between latitude 58°–60° N and longitude 22°–28° E. According to the Estonian Information System's Authority (2012), the total area of Estonia is 45,227 km², including 42,692 km² of land. More than one-half of the land area is forest, and one-third is agricultural land (arable land and natural grasslands). Approximately 8% is urban and infrastructure and the rest of the land is heathland, mires and bogs. Since 31 December 2010, 18.1% of Estonia has been under various types of nature protection (Environmental Information 2012).

By the end of 2011, the population of Estonia was 1.32 million and had decreased because of migration (Statistics Estonia 2012). Approximately 69% of the population live in the major towns and cities and 35 % of all live in semi-detached or detached houses, which traditionally have gardens. In 2010, the population density was 30.9 inhabitants per km². After 1 January 2011, the currency of Estonia was converted to the Euro, but during the research period for the present study the currency was the Estonian kroons (1 EUR = 15.6 EEK).

As mentioned above, national wealth is a key parameter in determining the likelihood of plant invasions. In 2011, the Gross Domestic Product per capita of Estonia was 20.2 US Dollars compared with 15.4 for Latvia and 38.3 for Finland. Estonia is, therefore, not in the highest wealth category, but it is still rich compared with countries outside Europe. However, the economy is growing, and gardening is a very popular activity, especially in the countryside where most houses have gardens. There is, therefore, a strong market for horticultural products.

In Estonia, horticulture, vegetable and fruit production have been concentrated in a relatively small number of businesses: approximately 2% of the total number of agricultural companies. There are no exact data on the numbers of nurseries in Estonia specialising in ornamental horticulture. The non-profit Estonian Horticultural Association (www.aiandusliit.ee) brings together companies that produce horticultural products for the market, as well as training and science institutions and companies retailing gardening accessories. There are about 80 members and from their occupational description it is estimated that approximately 25–30 of them are linked to the importation, cultivation on-site, and sale of herbaceous perennial species.

National regulations on (invasive) alien species

In Estonia, the principal authority on alien species is the Ministry of Environment, which is responsible for legislation and cooperation with international expert groups (e.g., NOBANIS, the Bern convention IAS group, and the EPPO IAS group). The Environmental Board is responsible for nature conservation activities and practical work with alien and invasive alien species.

The Nature Conservation Act (The State Gazette I, 2004, 38, 258) is the principal instrument that forbids the release of alien species into the wild. This Act has resulted in the definition of The List of Invasive Alien Species (Annex of The State Gazette 2004, 134, 2076). This regulation includes both well-established species and plants that are not yet established but which have caused problems in countries with similar environments. At present, this list includes 13 plant species. The import of live specimens and all transactions with live plants are prohibited for all these species.

The complete list of the texts on invasive species that have been implemented to date; including both those that are legally binding and those that are not; is presented in a report entitled "A Comparative Assessment of Existing Policies on Invasive Species in the EU Member States and in Selected OECD Countries" (European Commission 2011).

Methods

Sample of nurseries, database characteristics, statistical analysis

Seventeen nurseries located throughout Estonia were selected for this study. The choice was determined by the availability of catalogues. Firstly, an extensive list of cultivars and prices of herbaceous perennial species was compiled from catalogues, and the data was structured at the species, subspecies, and varietal or hybrid taxonomic level. In addition, basic information was collected for each taxon (Table 1), whenever such information was available. The species status in the Estonian Flora was determined from the Vascular Plant Flora of Estonia (Kukk 1999), where natives and archaeophytes are considered to be in the same group, i.e., natives. Hence, the alien species considered in this study were neophytes from this region. The alien species status (casual, naturalised and invasive) and other characteristics connected to alien species' invasiveness on Estonian territory were used as applied in Estonian Alien Flora (Ööpik et al. 2008), after which the invasive status of alien species was used in the sense proposed by Richardson et al. (2000) and Pyšek et al. (2004).

The complete description of species characteristics (Table 1) provides the basis for analysing the relationships between species status (native or alien: non-escaping, casual, naturalised, invasive), abundance in the wild, year of the first introduction (not available for non-escaping aliens), origin area of alien species (Kukk 1999), wholesale or retail price in 2010 (divided into ranges), and the number of nurseries in which the

Торіс	Characteristic	Categories used	
Species identity and	Genus, species, subspecies,		
taxonomic position	family		
Species status in Estonian		Native (1)	
Flora		Alien (2)	
Alien species investveness on		Non-escaping (1)	
Estonian territory and in the	Invasive status	Casual (2)	
neighbouring countries	invasive status	Naturalised (3)	
		Invasive (4)	
	Year of introduction		
	Year of the first record in the wild		
		Rare (1)	
	Abundance in the wild	Uncommon (2)	
	(frequency classes)	Scattered or occasional (3)	
		Common (4)	
	Invasiveness in NOBANIS	Potentially invasive or invasive in the	
	(qualitative characteristic)	region†	
		0- not mentioned as potentially invasive	
		or invasive; 1- potentially invasive or	
	Invasiveness in NOBANIS	invasive in one country. Values of 2 or	
	(quantitative characteristic)	greater denote the number of countries in	
		which the species is potentially invasive or	
		America, Asia, Europa, Eurasia	
	Area of origin (floristic element)	(continental), Euro-Siberia, Circumpolar,	
		from cultivation)	
	Species present on the list of a		
Nursery information (N=17)	certain nursery	0- not present; 1- present	
	Number of nurseries in which		
	the species is available		
	Number of cultivars per species		
	available		
		1 class up to 30 EEK (approx, 2 EUR)	
	Wholesale or retail price in	2 class 31-50 EEK (> 2 to 3.2 EUR)	
	2010 (divided into ranges)	3 class 51-100 EEK (> 3.2 to 6.4 EUR)	
		4 class greater than 100 EEK (> 6.4 EUR)	

Table 1. The content of the database of herbaceous perennial species available in the Estonian horticultural market describing the species characteristics and categories assigned to each individual species.

† Latvia, Lithuania, Finland, Sweden, Denmark, Norway, Poland, European part of Russia

species is available. Only one, and in the case of differences between nurseries, the highest price range category for each species was determined. The status of species in neighbouring countries was derived from the database of the European Network on Invasive Alien Species (NOBANIS, www.nobanis.org). In this database, invasive alien species are defined as those whose introduction and/or spread threaten biological diversity.

The STATISTICA software system ver. 11 (StatSoft, Inc. 2012) was used for all statistical analysis to perform a nonparametric Kruskal-Wallis ANOVA (*H* statistic),

an analysis of variance performed on ranks. Specifically, the different characteristics of multiple independent samples (groups) were compared. Species status was related to species price and to availability as well as alien species status, and abundance class to residence time. In addition, the multiple comparisons test was used to assess the mean ranks of all pairs of groups (see Siegel and Castellan 1988) and to compute post hoc measures of the mean ranks of all pairs of groups based on the *z* statistic. The correlation between price and availability, introduction time, and invasiveness in neighbour countries, was tested with nonparametric Spearman rank correlation (R).

List of species needing attention

As a practical application, a qualitative list of the nationally problematic species among the herbaceous perennials found in horticultural catalogues was compiled, based on data from local sources (Kukk 1999, Ööpik et al. 2008) and neighbouring countries (NOBANIS database) and on categories of multiple response characteristics as follows:

- (i) Invasive or naturalised in Estonia and invasive or potentially invasive in at least three neighbouring countries.
- (ii) Naturalised in Estonia and invasive or potentially invasive in two neighbouring countries.
- (iii) Naturalised in Estonia.
- (iv) Casual in Estonia, but invasive or potentially invasive elsewhere. These species are not addressed in this study.

The complete list of perennials in The List of Invasive Alien Species (The State Gazette Supplement 2004, 134, 2076) was also examined, to analyse whether the current legally valid list is applicable to everyday trade.

Results

General structure of the database

The database consists of 3,697 primary entries. These entries were analysed at the taxonomic level of species (N=779, 89% of all entries), subspecies (N=31), and variety or hybrid (N=70) to produce a list of 880 taxa (hereinafter called species). Of this list, 10.3% (91) are native species, 89.7% (789) alien species. Of all the aliens, 100 have been recorded outside cultivated areas and have reached a certain invasive status in Estonia - 62 are casuals, 35 naturalised, and 3 invasive species: *Lupinus polyphyllus* Lindl., *Saponaria officinalis* L. *and Solidago canadensis* L.. A total of 689 (87.3% of all aliens) are non-escaping species that are still confined to cultivated land. In all, the species belong to 73 families (Table 2) and 269 genera. The native species in the list are most

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Family	Native species	Non-escaping aliens	Casual aliens	Naturalised aliens	Invasive aliens	All
Asteraceae	10	98	16	8	1	133
Ranunculaceae	7	58	0	3	0	68
Lamiaceae	8	42	12	3	0	65
Caryophyllaceae	9	38	6	2	1	56
Rosaceae	8	36	3	3	0	50
Saxifragaceae	2	45	2	0	0	49
Crassulaceae	4	32	5	1	0	42
Primulaceae	2	32	0	2	0	36
Scrophulariaceae	4	26	3	1	0	34
Brassicaceae	0	22	1	0	0	23
Campanulaceae	5	15	0	0	0	20
Others	32	245	14	12	1	299
Total no of species	91	689	62	35	3	880
Total no of families	32	65	18	18	3	73

Table 2. The invasive status of perennial species available in the Estonian horticultural market, listed by family.

frequently represented by the genus *Campanula* L.. The most common genera among the alien taxa are *Sedum* L., *Saxifraga* L., *Aster* L., *Dianthus* L., and *Geranium* L..

According to their area of origin, 36% of the alien perennial species available on the horticultural market are native to Europe, Eurasia or Euro-Siberia. Approximately 30% are from Asia and 27% from the Americas.

The number of species per nursery varied from 41 to 383, and 44% of the species were present in only one nursery. Only one non-escaping alien, *Liatris spicata* (L.) Willd., was available from all 17 nurseries. *Bergenia cordifolia* (Haw.) Sternb. and *Echinacea purpurea* (L.) Moench (both non-escaping aliens) were available from 16 nurseries, and the native *Ajuga reptans* L. was available from 15 nurseries. The mixture in each nursery was quite similar: 10–20% natives, 60–80% non-escaping aliens, 10% casuals, 2–10% naturalised. Eight nurseries offered invasive species. The largest and most variable category was non-escaping alien species (Figure 1).

The results show that approximately 70% of the species had no cultivars or only one type available for sale. Only 43 (4.9%) of the species had ten or more cultivars per species. The outstanding favourite species was the non-escaping alien *Hemerocallis hybrida* hort. with 134 different varieties, followed by *Sempervivum x hybridum* hort. (68), *Phlox paniculata* L. (65), and the naturalised alien *Iris germanica* L. (42).

Market characteristics and species invasiveness

The results show that two groups - native and alien species found outside cultivation of any status from casual to invasive - have a similar market profile, in contrast to nonescaping alien species. Alien species that are able to escape and reach certain invasive



Figure 1. The number of species per nursery (N = 17) according to species status in Estonia. The results are presented in terms of the extreme values of the data and the median. In addition, three invasive species are offered in catalogues of eight different nurseries.

status in Estonia, are today less expensive (H = 13.9, DF = 2, N = 668, p = 0.001; Figure 2) and also more widely available (H = 32.6, DF = 2, N = 880, p < 0.0001; Figure 3) than those that have not escaped. In all, the price range of the species is lower when it is widely available and vice versa (R = -0.36, p < 0.05). Also, native and escaping alien species have more developed cultivars per species available on the market (H = 13.26, DF = 2, N = 880, p = 0.001). The latter is also positively correlated to number of nurseries where the species is available (R = 0.66, p < 0.05). In addition, when a species has already reached a certain invasive status in the alien flora, then the price (H = 0.02, DF = 2, N = 86, p = 0.7), availability (H = 0.64, DF = 2, N = 100, p = 0.7) and a number of cultivars per species (H = 2.52, DF = 2, N = 100, p = 0.28) does not differ between groups of casual, naturalised and invasive aliens.

Among the already escaped alien species, the abundance (H = 12.3, DF = 3, N = 83, p = 0.007; Figure 4a) and invasive status of species (H = 10.4, DF = 2, N = 86, p = 0.006; Figure 4b) tends to increase with residence time. Invasiveness in the whole region (see Table 1) is also significantly correlated to the year of introduction into Estonia (R = -0.33, p < 0.05), to the species status in Estonia (R = 0.52, p < 0.05) and to the abundance in the wild (R = -0.47, p < 0.05). The supply and demand factors, i.e. today's availability (R = 0.02, p > 0.05) and price range of alien species in Estonian alien flora (R = 0.08, p > 0.05), is not correlated with introduction time.



Figure 2. The relationship between species price and status in 17 nurseries in Estonia. Non- escaping aliens were more expensive than natives (z' = 2.7, p < 0.05) and species in certain status (casual, naturalised, invasive) in alien flora (z' = 2.8, p = 0.02).



Figure 3. The relationship between species status and availability in 17 nurseries in Estonia. Non-escaping alien species were different from natives (z' = 4.9, p = 0.007) and aliens in spontaneous flora (z' = 3.03, p < 0.0001).



Figure 4. The relationship between alien species characteristics and residence time in 17 nurseries in Estonia: (**A**) species abundance in the wild and residence time (general test was statistically significant (see text), but no significant differences between groups were detected because of small sample sizes), (**B**) alien species status and residence time. The residence time of casuals were shorter than of naturalised species (z' = 3.72, p = 0.0006). Sample of invasive species was too small to drive statistically significant conclusions.

Table 3. Estonian commercial nurseries offering herbaceous perennial species, which need national attention as invasive or potentially invasive aliens. Category I: invasive or naturalised species in Estonia and invasive or potentially invasive in at least three neighbouring countries. Category II: naturalised in Estonia and invasive or potentially invasive in two neighbouring countries. Category III: naturalised in Estonia.

Species in category I	Species in category II	Species in category III
Lupinus polyphyllus Lindl.	Aster novi-belgii L.	Aquilegia vulgaris L.
Solidago canadensis L.†	Euphorbia cyparissias L.	Astrantia major L.
Saponaria officinalis L.	Inula helenium L.	Cymbalaria muralis P. Gaertn. et al.
<i>Fallopia japonica</i> (Houtt.) Ronse Dec.†	Sedum spurium M.Bieb.	Delphinium elatum L.
<i>Fallopia sachalinensis</i> (F.Schmidt) Ronse Decr.†	Aconitum napellus L.	Dipsacus fullonum L.
Echinops sphaerocephalus L.	Aruncus dioicus (Walter) Fernald	Doronicum pardalianches L.
Telekia speciosa (Schreb.) Baumg.	Bellis perennis L.	Echinops ritro L.
Vinca minor L.	Dianthus barbatus L.	Iris germanica L.
	<i>Fragaria x ananassa</i> Duchesne	Mentha spicata L.
	Lychnis chalcedonica L.	Nepeta cataria L.
	Malva alcea L.	Ornithogalum umbellatum L.
	<i>Rudbekia laciniata</i> L.	Physalis alkekengi L.
	Salvia verticillata L.	Primula elatior (L.) Hill
	<i>Viola odorata</i> L.	Primula vulgaris Huds.
		Sanguisorba minor Scop.
		Sisyrinchium angustifolium Mill.

[†] Species are on The List of Invasive Alien Species (Regulation of the Estonian Minister of Environment No 34, 14 May 2007) - importing live specimens and all transactions with live specimens are prohibited, as stated in The Nature Conservation Act.

List of species needing attention

As a practical application, a qualitative list of the nationally problematic species among the herbaceous perennials in horticultural catalogues was compiled (Table 3). In Estonia, The Nature Conservation Act forbids the release of alien species into the wild. This Act has resulted in the definition of The List of Invasive Alien Species. For all these species, the import of live specimens and all transactions with live plants are prohibited. As a result, three species are on both the compiled list and the legally defined list.

Discussion

It is generally accepted that only a limited fraction of introduced species in a given area become naturalised and an even smaller number eventually cause problems (Williamson and Fitter 1996, see also Jeschke et al. 2012). However, initially it is not usually possible to speculate about the potential magnitude of these introductions. The results of the present study demonstrate that the total introduced number of 789 alien herbaceous perennial species available in Estonian commercial nurseries compares with the 787 alien species in the entire Estonian Alien Flora (Ööpik et al. 2008). Species chosen for their ornamental attraction do not necessarily have more invasive potential than other comparable plants, but the proportionally large number of all introduced species increases the likelihood that a fraction will become naturalised and even invasive (see also Mack 2003). The situation should be therefore monitored carefully.

Invasions have a highly dynamic nature, and many of the most problematic alien species are not recent arrivals, but they reflect historical human activities, a phenomenon termed an invasion debt (Essl et al. 2011). One part of this reflection is species residence time in the given area: the longer the species is present in the area, the more propagules are spread and the probability of naturalisation increases (Rejmánek et al. 2005). Unfortunately, in real-life situations the actual introduction time is usually unknown or not determined and for this study were available only years of introduction for alien species in alien flora (Ööpik et al. 2008). Nevertheless, the data in the present paper support the generalisation that the residence time affects the range and frequency, as well as the invasive status, of alien species, at least in cases where the species have already reached a status in spontaneous flora. Also, quite often the most effective predictors of invasiveness were "invasive elsewhere" (Herron et al. 2007). Our data show that the invasive status in Estonia, abundance in the wild and of course, the year of introduction into Estonia correlates with current invasiveness of the species in the whole region. Thus, the regional cooperation in this field should be favoured.

Recently, it has been shown that residence time is a pivotal factor in the spatial patterns of alien species and human pressure has a greater influence on species that have been introduced more recently (Dainese and Poldini 2012). For the future studies we hypothesise here that exponential growth of trade and travel and various pressures from current consumption could decrease the importance of residence time; further, naturalisations and even invasions will take place quicker and be more dependent on other human-mediations than at present.

Propagule pressure created by the historic factors of supply and demand is also an important part of the explanation for the invasiveness of ornamental species (Dehnen-Schmutz et al. 2007b, Pemberton and Liu 2009). Hence, the current lists have the present levels of socio-economic activity as a background and suggest the possibility of future invasions. Nevertheless, according to the study data, native and expanding wild alien species have today a similar market profile, as they are both inexpensive and widely available. This could be a robust reflection from the previous planting history of alien species, because today's price or availability does not differ between groups of casual, naturalised or invasive aliens. Also, among species in alien flora the introduction time does not predict today's lower price or wider availability. All the species which have currently reached status in spontaneous flora are similarly favoured on the market as "easy-to-grow" species. Such plants are often popular, because they may be readily propagated, and hence are usually less expensive. However, a history of active planting and repeated introductions creates additional pressure and may result in rapid rates of spread, successful escape of species from cultivation and subsequent naturalisation.

The objective of breeding plants to encourage specific traits differs between agriculture and ornamental horticulture. Obviously, bred ornamental cultivars are genetically distinct from the wild genotype of the species, but usually the change in genetic composition is minor and has little to do with the traits that lead species to become naturalised and invasive (Reichard 2011). Nevertheless, for a few species, recent molecular evidence suggests that continuing propagule pressure aids the spreading of an invasion by introducing genetic variation adaptive for new areas and habitats (Simberloff 2009). In this paper, selection strategies to reduce the invasive potential in introduced plants (Anderson et al. 2006) are not considered. Instead, it is suggested that the number of cultivars per species is likely to be strongly correlated with the number of nurseries where that species is available and will provide an additional opportunity to escape from cultivation. In this case there is another dimension of generated human-mediated propagule pressure. When more cultivars come on the market, then inevitably there will be more specimens in more sites to act as potential dispersers, which is the classical explanation of propagule pressure (Simberloff 2009).

The financial costs to countries of controlling the major invasive species are very high and pose serious problems (Pimentel et al. 2005); hence, regulations are needed. In theory, the control of international release should be straightforward. However, such control is practically difficult due to the financial pressure resulting from the modern global trade in plants. In general, an appropriate framework should enable the trends to be monitored and accept the control of future introductions (e.g., Hulme et al. 2008). There are also difficulties with the negotiation of international agreements. Such difficulties occur within the European Union and are even more pronounced on a global scale.

The one pro-active possibility is that green lists should be compiled. These lists would be especially useful in large-scale projects and would not contradict any trade agreements (Dehnen-Schmutz 2011). In Estonia, The Nature Conservation Act forbids the release of alien species into the wild and The List of Invasive Alien Species prohibits the import of specimens and all transactions with live plants. Currently this list includes 13 plant species, which differ significantly - some species are well-established and some are not yet introduced into Estonia, but have caused problems in countries with similar environments. Unfortunately, the results of this paper show that the compiled list of more problematic species in Estonia and in neighbouring countries include altogether 38 species (Table 3). Three regionally problematic species, Solidago canadensis, Fallopia japonica, Fallopia sachalinensis, are available on the Estonian market and are at the same time on the legally prohibited list. Thus, even though the country has quite strict existing regulations, they are not entirely enforced; currently Estonia is only beginning systematic work in this field. It has been proposed that voluntarily implemented Codes of Conduct (Heywood and Brunel 2006) which are addressed to governments, to the horticultural industry and trade, to local environment and conservation agencies, societies and associations, botanic gardens, etc., can be better alternatives to regulate this situation comprehensively. At a national level, a few European countries have addressed the issues of invasive alien species and horticulture and developed a strategy (see references in Heywood and Brunel 2011, p. 19-20).

Why should the horticultural industry care about alien species? This question arises because the problems caused by alien species do not have a substantial impact on the industry. For this reason, it is probable that further regulation will be difficult. An economical study by Knowler and Barbier (2005) has suggested the possibility of employing market-based instruments consistent with the concept of 'introducers-pay', to regulate the nursery industry. Yokomizo et al. (2012) proposed a cost-benefit analysis for determining plant introduction that incorporates probability to escape, expected economic cost after escape, expected commercial benefits, and the efficiency and cost of containment. Details of the structural changes required, are given by Dehnen-Schmutz et al. (2010), who also emphasise the complexity of the situation. Drew et al. (2010) and Peters et al. (2006) have both suggested that the involvement of consumers and also professionals, as well as education, may yield better results by addressing the moral problem of the risks caused by alien species and understanding the characteristics of the industry. Different voluntary initiatives and regulations are often quite effective and should be increased to limit horticultural introductions of invasive plants (Burt et al. 2007, Niemiera and Von Holle 2009). Some results suggested that merely labelling the plants as invasive or native could be a viable strategy for changes in customer behaviour (Yue et al. 2011). Control measures should at least be part of any overall framework, if there is agreement to implement regulations. However, in nature as in economics, there are always cost-benefit trade-offs.

Conclusions

- 1) The availability of plants from the horticultural trade is a major source of alien species, including locally and regionally naturalised and invasive plants.
- 2) Supply and demand factors create new and reflect previous propagule pressure and are an important component of the reasons behind the invasiveness of ornamental species. In general, native and expanding wild alien species have a very similar profile on the market - both are inexpensive and widely available, and more cultivars per species are also available.
- 3) There are urgent requirements for regional and national authorities to regulate and control the ornamental plant trade in order to diminish the risk of new invasions.
- 4) It would be helpful to involve the public in finding alternatives and encouraging best practices for both horticultural professionals and amateurs.

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References

- Anderson NO, Galatowitsch SM, Gomez N (2006) Selection strategies to reduce invasive potential in introduced plants. Euphytica 148: 203–216. doi: 10.1007/s10681-006-5951-7
- Barbier EB, Gwatipedza J, Knowler D, Reichard S (2011) The North American horticultural industry and the risk of plant invasion. Agricultural Economics 42: 113–129. doi: 10.1111/j.1574-0862.2011.00556.x
- Beans CM, Kilkenny FF, Galloway LF (2012) Climate suitability and human influences combined explain the range expansion of an invasive horticultural plant. Biological Invasions: 14: 2067–2078. doi: 10.1007/s10530-012-0214-0
- Bucharova A, van Kleunen M (2009) Introduction history and species characteristics partly explain naturalization success of North American woody species in Europe. Journal of Ecology 97: 230–238. doi: 10.1111/j.1365-2745.2008.01469.x
- Burt JW, Muir AA, Piovia-Scott J, Veblen KE, Chang AL, Grossman JD, Weiskel HW (2007) Preventing horticultural introductions of invasive plants: potential efficacy of voluntary initiatives. Biological Invasions 9: 909–923. doi: 10.1007/s10530-007-9090-4
- Chrobock T, Kempel A, Fischer M, van Kleunen M (2011) Introduction bias: Ciltivated alien plant species germinate faster and more abundantly than native species in Switzerland. Basic and Applied Ecology 12: 244–250. doi: 10.1016/j.baae.2011.03.001
- Dainese M, Poldini L (2012) Does residence time affect responses of alien species richness to environmental and spatial processes? NeoBiota 14: 47–66. doi: 10.3897/neobiota.14.3273
- Dehnen-Schmutz K (2011) Determining non-invasiveness in ornamental plants to build green lists. Journal of Applied Ecology 48: 1374–1380. doi: 10.1111/j.1365-2664.2011.02061.x
- Dehnen-Schmutz K, Holdenrieder O, Jeger MJ, Pautasso M (2010) Structural change in the international horticultural industry: Some implications for plant health. Scientia Horticulturae 125: 1–15. doi: 10.1016/j.scienta.2010.02.017
- Dehnen-Schmutz K, Touza J, Perrings C, Williamson M (2007a) The horticultural trade and ornamental plant invasions in Britain. Conservation Biology 21: 224–231. doi: 10.1111/j.1523-1739.2006.00538.x
- Dehnen-Schmutz K, Touza J, Perrings C, Williamson M (2007b) A century of the ornamental plant trade and its impacts on invasion success. Diversity and Distribution 13: 527–534. doi: 10.1111/j.1472-4642.2007.00359.x
- Drew J, Anderson N, Andow D (2010) Conundrums of a complex vector for invasive species control: a detailed examination of the horticultural industry. Biological Invasions 12: 2837–2851. doi: 10.1007/s10530-010-9689-8

Environmental Information (2012) www.keskkonnainfo.ee

- Essl F, Dullinger S, Rabitsch W, Hulme PE, Hülber K, Jarošik V, Kleinbauer I, Krausmann F, Kühn I, Nentwig W, Vilà M, Genovesi P, Gherardi F, Desprez-Loustau M-L, Roques A, Pyšek P (2011) Socioeconomic Legacy yields an invasion debt. PNAS 108 (1): 203–207. doi: 10.1073/pnas.1011728108
- Estonian Information System's Authority (2012) http://www.ria.ee/en/

- European Commission (2011) A comparative assessment of existing policies on invasive species in the EU Member States and in selected OECD countries. Bio Intelligence Service: 86–98.
- Hanspach J, Kühn I, Pyšek P, Boos E, Klotz S (2008) Correlates of naturalization and occupancy of introduced ornamentals in Germany. Perspectives in Plant Ecology, Evolution and Systematics 10: 241–250. doi: 10.1016/j.ppees.2008.05.001
- Herron PM, Martine CT, Latimer AM, Leicht-Young SA (2007) Invasive plants and their ecological strategies: prediction and explanation of woody plant invasion in New England. Diversity and Distributions 13: 633–644. doi: 10.1111/j.1472-4642.2007.00381.x
- Heywood V, Brunel S (2011) Code of Conduct on Horticulture and Invasive Alien Plants. Nature and environment 162. Council of Europe Publishing, Strasbourg.
- Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. Journal of Applied Ecology 46: 10–18. doi: 10.1111/j.1365-2664.2008.01600.x
- Hulme PE, Bacher S, Kenis M, Klotz S, Kühn I, Minchin D, Nentwig W, Olenin S, Panov V, Pergl J, Pyšek P, Poques A, Sol D, Solarz W, Vilà M (2008) Grasping at the routes of biological invasions: a framework for integrating pathways into policy. Journal of Applied Ecology 45: 403–414. doi: 10.1111/j.1365-2664.2007.01442.x
- Jeschke JM, Gómez Aparicio L, Haider S, Heger T, Lortie CJ, Pyšek P, Strayer DL (2012) Support for major hypotheses in invasion biology is uneven and declining. NeoBiota 14: 1–20. doi: 10.3897/neobiota.14.3435
- Niemiera AX, Von Holle B (2009) Invasive Plant Species and the Ornamental Horticulture Industry. In: Inderjit (Ed) Management of Invasive Weeds.
- Knowler D, Barbier E (2005) Importing exotic plants and the risk of invasion: are market-based instruments adequate? Ecological Economics 52: 341–354. doi: 10.1016/j. ecolecon.2004.06.019
- Kowarik I (2003) Human agency in biological invasions: secondary releases foster naturalisation and population expansion of alien plant species. Biological Invasions 5: 293–312. doi: 10.1023/B:BINV.0000005574.15074.66
- Kukk T (1999) Vascular plant flora of Estonia. Teaduste Akadeemia Kirjastus, Tartu-Tallinn. [In Estonian with English summary]
- Küster EC, Kühn I, Bruelheide H, Klotz S (2008) Trait interactions help explain plant invasion success in the German flora. Journal of Ecology 96: 860–868. doi: 10.1111/j.1365-2745.2008.01406.x
- Lockwood JL, Cassey P, Blackburn TM (2009) The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. Diversity and Distribution 15: 904–910. doi: 10.1111/j.1472-4642.2009.00594.x
- Mack RN (2000) Cultivation fosters plant naturalization by reducing environmental stochasticity. Biological Invasions 2: 111–122. doi: 10.1023/A:1010088422771
- Mack RN (2003) Global plant dispersal, naturalization, and invasion: pathways, modes, and circumstances. In: Ruiz GM, Carlton JT (Eds) Invasive species: vectors and management strategies, pp. 3–30. Island Press, Washington.

- Mack RN, Erneberg M (2002) The United States Naturalized Flora: Largely the Product of Deliberate Introductions. Annals of the Missouri Botanical Garden 89(2): 176–189. URL: http://www.jstor.org/stable/3298562
- Mack RN, Lonsdale WM (2001) Humans as global plant dispersers: getting more than we bargained for. BioScience 51: 95–102. doi: 10.1641/0006-3568(2001)051[0095:HAGP-DG]2.0.CO;2
- Marco A, Lavergne S, Dutoit T, Bertaudiere-Montes V (2010) From the backyard to the backcountry: how ecological and biological traits explain the escape of garden plants into Mediterranean old fields. Biological Invasions 12: 761–779. doi: 10.1007/s10530-009-9479-3
- Milbau A, Stout JC (2008) Factors Associated with Alien Plants Transitioning from Casual, to Naturalized, to Invasive. Conservation Biology 22: 308–317. doi: 10.1111/j.1523-1739.2007.00877.x
- NOBANIS, European Network of Invasive Alien Species. www.nobanis.org
- Ööpik M, Kukk T, Kull K, Kull T (2008) The importance of human mediation in species establishment: analysis of alien flora of Estonia. Boreal Environment Research 13(A): 53–67.
- Pemberton RW, Liu H (2009) Marketing time predicts naturalization of horticultural plants. Ecology 90: 69–80. doi: 10.1890/07-1516.1
- Peters WL, Hockenberry Mayer M, Andreson NO (2006) Minnesota horticultural industry survey on invasive plants. Euphytica 148: 75–86. doi: 10.1007/s10681-006-5942-8
- Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien species in the United States. Ecological Economics 52: 273–288. doi: 10.1016/j.ecolecon.2004.10.002
- Pyšek P, Jarošík V, Hulme PE, Kühn I, Wild J, Arianoutsou M, Bacher S, Chiron F, Didžiulis V, Essl F, Genovesi P, Gherardi F, Hejda M, Kark S, Lambdon PW, Desprez-Loustau M-L, Nentwig W, Pergl J, Poboljšaj K, Rabitsch W, Roques A, Roy DB, Shirley S, Solarz W, Vilà M, Winter M (2010) Disentangling the role of environmental and human pressures on biological invasions across Europe. PNAS 107: 12157–12162. doi: 10.1073/ pnas.1002314107
- Pyšek P, Jarošík V, Pergl J (2011) Alien Plants Introduced by Different Pathways Differ in Invasion Success: Unintentional Introductions as a Threat to Natural Areas. PLoS ONE 6(9): e24890. doi: 10.1371/journal.pone.0024890
- Pyšek P, Richardson DM (2007) Traits associated with invasiveness in alien plants: where do we stand? In: Nentwig W (Ed) Biological Invasion. Springer, Berlin, 97–125. doi: 10.1007/978-3-540-36920-2_7
- Pyšek P, Richardson DM, Rejmánek M, Webster GL, Williamson M, Kirschner J (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. Taxon 53(1): 131–143. doi: 10.2307/4135498
- Reichard SH, White P (2001) Horticulture as a pathway of invasive plant introductions in the United States. BioScience 51: 103–113. doi: 10.1641/0006-3568(2001)051[0103:HAA POI]2.0.CO;2
- Reichard S (2011) Horticulture. In: Simberloff D and Rejmanek M (Eds) Encyclopedia of Biological Invasions. University of California Press, 336–342.
- Rejmánek M, Richardson DM, Pyšek P (2005) Plant invasions and invasibility of plant communities. In: van der Maarel E (Ed.) Vegetation ecology. Blackwell Publishing, Cornwall, UK, pp.
- Richardson DM, Pyšek P (2012) Naturalization of introduced plants: ecological drivers of biogeographical patterns. New Phytologist 196: 383–396. doi: 10.1111/j.1469-8137.2012.04292.x
- Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6: 93–107. doi: 10.1046/j.1472-4642.2000.00083.x
- Siegel S, Castellan NJ (1988) Nonparametric statistics for the behavioral sciences (2nd ed.) New York: McGraw-Hill.
- Simberloff D (2009) The role of propagule pressure in biological invasions. Annual Review of Ecology, Evolution, and Systematics: 40: 142–149. doi: 10.1146/annurev.ecolsys.110308.120304
- Smith RM, Thompson K, Hodgson JG, Warren PH, Gaston KJ (2006) Urban domestic gardens (IX): Composition and richness of the vascular plant flora, and implications for native biodiversity. Biological Conservation 129: 312–322. doi: 10.1016/j.biocon.2005.10.045
- Starfinger U, Kowarik I, Rode M, Schepker H (2003) From desirable ornamental plant to pest to accepted addition to the flora? – the perception of an alien tree species through the centuries. Biological Invasions 5: 323–335. doi: 10.1023/B:BINV.0000005573.14800.07 Statistics Estonia (2012) http://www.stat.ee/
- StatSoft, Inc (2012) STATISTICA (data analysis software system), version 11. www.statsoft.com
- The List of Invasive Alien Species, Annex of The State Gazette 2004, 134, 2076. https://www.riigiteataja.ee/akt/12828512 [In Estonian]
- The Nature Conservation Act, The State Gazette I, 2004, 38, 258. https://www.riigiteataja.ee/akt/12808270 [In Estonian]
- Thuiller W, Richardson DM, Rouget M, Proches S, Wilson J (2006) Interaction between environment, species traits, and human uses describe patterns of plant invasions. Ecology 87: 1755–1769. doi: 10.1890/0012-9658(2006)87[1755:IBESTA]2.0.CO;2
- Trueman M, Atkinson R, Guézou A, Wurm P (2010) Residence time and human-mediated propagule pressure at work in the alien flora of Galapagos. Biological Invasions 12: 3949– 3960. doi: 10.1007/s10530-010-9822-8
- Weber E (2003) Invasive plant species of the world: a reference guide to environmental weeds. CABI Publishing.
- Williamson M, Fitter A (1996) The varying success of invaders. Ecology 77: 1661–1666. http://www.jstor.org/stable/2265769
- Yokomizo H, Possingham HP, Hulme PE, Grice AC, Buckley YM (2012) Cost-benefit analysis for intentional plant introductions under uncertainty. Biological Invasions 14: 839–849. doi: 10.1007/s10530-011-0120-x
- Yue C, Terrance MH, Anderson N (2011) Do native and invasive labels affect consumer willingness to pay for plants? Evidence from experimental auctions. Agricultural Economics 42: 195–205. doi: 10.1111/j.1574-0862.2010.00510.x

RESEARCH ARTICLE



Do species differ in their ability to coexist with the dominant alien *Lupinus polyphyllus*? A comparison between two distinct invaded ranges and a native range

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Abstract

The community-level impacts of invasive plants are likely to vary depending on the character of native species of the target communities and their ability to thrive within the stands of the dominant alien invader. Therefore, I examined the response of native species richness to the cover of the dominant alien *Lupinus polyphyllus* in two distinct invaded ranges: Czech Republic (Central Europe) and New Zealand. I compared the relation between native species richness and the cover of the dominant alien *L. polyphyllus* with that in its native range, Pacific Northwest, USA.

In the native range, I found no response of native species richness to the cover of *L. polyphyllus*. In the Czech Republic (central Europe), the richness of native species related to it negativelly, but the relation was only marginally significant. Contrary to that, the richness of species native to New Zealand related to the cover of *L. polyphyllus* strongly negatively and the negative relation was significantly stronger than that of species native to Europe.

Of the two invaded ranges, species native to New Zealand have been documented to be much more vulnerable to the conditions associated with the invasion and dominance of *L. polyphyllus*, compared to species native to central Europe. This principle has been shown both across these two invaded ranges and in New Zealand, where the aliens of european origin successfully coexist with the dominant invasive alien *L. polyphyllus*. Similarly, species in the native range of *L. polyphyllus* showed no relation to its cover, indicating their ability to thrive even in dense stands of this dominant species.

Keywords

Lupinus polyphyllus, invasive alien species, native range, invaded range, coexistence of species, diversity, dominance

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Introduction

Invasions of alien plant species have become widely recognized as one of the major human-induced changes, affecting the whole biosphere at the global scale (Tilman 1999, Manchester and Bullock 2000). In the last decade, the attention has been focused on testing, documenting and quantifying the impacts of alien invasive species upon the resident communities (Mack et al. 2000, Davis 2003, Hejda et al. 2009, Vilà et al. 2010).

It has been documented that the character of the recipient community co-determines the magnitude of the alien's impact on diversity and, therefore, a single invasive species can have different impacts in different types of invaded communities (Mason and French 2008). Hejda et al. (2009) suggested that the impact on diversity of native species is especially strong, if the invader represents a novel and distinctive dominant to the community that has been lacking such dominants before the invasion. Some alien species, like *Impatiens glandulifera* or *Helianthus tuberosus*, have been documented to compete with native dominants without actually changing the site conditions for other native species, which results in relatively mild impacts on diversity, especially when considering these aliens' robust stature and tendency to grow in high densities. On the contrary, other invaders (*Fallopia* sp. div., *Heracleum mantegazzianum, Rumex alpinus*) have been documented to represent distinctive and novel dominants to the invaded communities and also to impact both diversity and composition of native species substantially (Hejda et al. 2009).

Aliens can alter conditions on large areas, such as when a tree species invades a formally treeless environment, as documented on Galápagos by Järger et al. (2007). At the same time, invasive aliens are often strong competitors and are able to exclude native species at fine scales, due to e. g. competition by roots, allellopathic compounds or by production of large amounts of above-ground biomass.

This paper aims to test the ability of native species to coexist with the dominant alien *Lupinus polyphyllus* and attempts to test the following hypotheses:

Do species of native and invaded ranges differ in their ability to thrive on sites with high dominance of *L. polyphyllus*?

Do native species of different invaded ranges (Czech Republic, central Europe; New Zealand) differ in their ability to coexist with the dominant invasive alien *L. polyphyllus*?

Methods

Study species

Lupinus polyphyllus is a 0.7 - 1.2 m tall, robust, rhizomatous perennial native to the Pacific Northwest of USA. In its native range, *L. polyphyllus* has been reported to grow in wet montane meadows, along streams, but also as a viatic weed. Despite *L. polyphyllus* being poisonous, there have been attempts to use it as fodder plant and low-alcaloid varieties have been introduced (Aniszewski 1993, Payne et al. 2004).

For ornamental and landscape purposes, *L. polyphyllus* was intentionally introduced to many regions of the world and has become invasive in central and northern Europe, Southern island of New Zealand and Tasmania. In the Czech Republic, *Lupinus polyphyllus* invades wet montane and submontane meadows, river banks and forest edges (Slavík et al. 1995). Both in its native and invaded ranges, the occurrence of *L. polyphyllus* seems to respond to human-induced disturbance positivelly and it often grows along roads and in other anthropogenically impacted places (see for example Valtonen et al. 2003). At the same time, *L. polyphyllus* is apparently able to colonize even rather extreme sites, with rocky and unstable substrates, periods of stress and / or low nutrient levels. This can be seen in New Zealand especially, where *L. polyphyllus* often colonizes frequently disturbed and rocky terraces of montane and submontane rivers (Holdaway and Sparrow 2006). The ability of *L. polyphyllus* to grow on lownutrient substrates is associated with its ability to utilize nitrogen from the air, which gives it a competitive advantage over nitrogen non-fixing species and makes it able to gain dominance even in oligotrophic conditions (Scott 2007).

The community-level impacts of *Lupinus polyphyllus* as an invasive alien have been studied in both Europe (Valtonen et al. 2006, Hejda et al. 2009) and New Zealand (Holdaway and Sparrow 2006). In SE Finland, *L. polyphyllus* was found to reduce road verge communities and the loss of diversity was documented on vascular plants and butterflies (Valtonen et al. 2006). In New Zealand, *L. polyphyllus* was documented to affect the succession series on river terraces by accumulating silt material and stabilising the riparian terraces (Holdaway and Sparrow 2006). In the native range, the ability of lupins to stabilize unstable soil and raise nutrient levels was documented on a related species *L. lepidus* on bare soils around Mt. St. Helen's (Del Moral and Rozzell 2005). In this case, lupins were found to facilitate conditions for the colonisation of other species.

The invasion of lupins is apparently promoted by the intentional introduction of generalist pollinators, such as bees or bumble-bees (Lye et al. 2010). In Tasmania, a related alien species *L. arboreus* was reported to be almost exclusively pollinated by introduced pollinators (Stout et al. 2002).

Study area

I carried out this comparative study in the native range of *L. polyphyllus*, which is the Pacific Northwest of USA, and two distinct invaded ranges (Southern Island of New Zealand and Czech Republic, central Europe).

In the native range, I sampled the data in the states of Washington and Oregon, USA. In Washington, the data were clustered around Mt. Rainier and Mt. Adams, while in Oregon, I sampled the data in the Columbia river Gorge around Bridal Veils. In New Zealand, I sampled the data on riparian meadows around the Waimakariri river, Arthur's Pass National park and around Eglington river, Fjordland National Park, Southern Island. In the Czech Republic, I sampled the data in Jizerské hory (NE Bohemia) and Slavkovský les (W Bohemia) natural and landscape reserves and around the town of Průhonice (central Bohemia). In all of these three ranges, I collected the data in mesic to wet meadows. All areas revealed relatively high precipitation and were not prone to summer drought periods.

It was not possible to locate the vegetation plots randomly, mainly because of spatially autocorrelated distribution of *L. polyphyllus* in the invaded ranges. In the Czech Republic and especialy in New Zealand, *L. polyphyllus* was found to be excessively abundant in some areas, whereas it was absent in other areas. This type of strongly autocorrelated spatial distribution leads to the plots being clustered in the areas, where *L. polyphyllus* was abundant and where it was observed to massively invade near-natural communities and compete with native species. The aim was to sample vegetation with a wide scale of *L. polyphyllus*' cover (dominance) in each area of its occurence. The GPS coordinates of plots are available in Appendix I.

Sampling design and data analysis

In all of the three ranges, I collected a dataset of 40 plots of an area of $2 \times 2m$ with varying cover of *L. polyphyllus*. I used the fine-scale plots because the aim of the project was to test the ability of species to thrive within the dense and homogenous stands of *L. polyphyllus*. On larger scales, the stands of *L. polyphyllus* tend to be patchy rather than homogenous, so the results would be biased by native species' growing in these empty patches rather than within the stands of *L. polyphyllus*. I recorded the present species and estimated their relative abundances on a percentage scale. Altogether, I sampled 120 plots of communities with L. polyphyllus from the three ranges together, plus 40 plots with the alien dominant Hieracium pilosella agg. and 40 plots with the alien dominant Anthoxantum odoratum in New Zealand, which makes 200 plots altogether. I estimated the dominance of lupins (and other alien dominants in New Zealand) as its percentage cover, which can be assumed to be a quick and easy to get proxy for biomass. At fine spatial scale, I selected sites with comparable conditions (light, stability and moisture of substrate, degree of ruderalization), in order to minimize the likelihood that the cover of lupins would be confounded with other basic environmental factors, biasing the results. I found the taxonomy of Lupins to be very complicated in the native range (Pacific Northwest, USA) and I had to exclude several plots from the dataset, leading to merely 22 plots from the native range. Lupins on the excluded plots were probably hybrids between L. polyphyllus and other related species, such as L. latifolius and L. burkei. Although these hybrids between L. polyphyllus and closelly related species were of similar appearance with robust stature and rhizomatous growth, they could have impacted the coexisting species differently, due to differences in e. g. nitrogen fixation rate or production of allellopathic compounds. For these reasons, I decided to keep the taxonomic delimitation of L. polyphyllus as consistent as possible across the ranges where the plots were sampled, however, leading to just 102 plots with L. *polyphyllus* used in the data analysis, compared to the originally intended 120.

I tested the response of species richness to the cover of lupins (and to the cover of *Anthoxantum odoratum* and *Hieracium pilosella* agg. in New Zealand) using Pearson correlations and the linearity of these relations using regression models. Further, I tested the differences in the response between various subsets of species (native to USA, native to Europe and native to New Zealand) by the mixed-effect analysis of covariance (Crawley 2007). In this model, the identity of spatial cluster (area within each range - see Appendix I) was the random effect, while the cover of *L. polyphyllus* (continuous variable) and the type of range (native range - USA, Czech Republic, New Zealand – factor variables) were the fixed effects. The interactions between the continuous term (cover of *L. polyphyllus*) and the category variables (native range, invaded ranges) was of the most interest, since it would reveal possible differences in the response of various subsets of species.

I used the ratios in the numbers of species between each plot and the most diverse plot sampled within the category of plots (USA, Czech Republic, New Zealand) as response variables. The plot with the maximum species richness within a particular category had an importance value of 1, while the other plots from this subgroup had importance values between 0 - 1, when the zero value says no species were recorded besides *L. polyphyllus* and the value of 1 says the plot harboured the same number of species as the plot with maximum species richness within that category. I did this because plots from the three ranges differed in native species richness substantially, with the invaded stands from New Zealand harbouring much less native species compared to the stands in either the Czech Republic or in the native range, USA. In other words, the difference of 5 native species between the least and most invaded stands represents a very different portion of native species richness recorded in New Zealand and in the Czech Republic. Therefore, I considered these ratios, representing portions of species thriving on a particular plot from the maximum sampled within each category of plots, as more relevant than simple numbers of species.

A separate mixed-effect regression model was created to test the response of native vs. alien species (of european origin exclusively) to the cover of *L. polyphyllus* in New Zealand. In this regression model, the identity of sampling areas in New Zealand (Arthur Pass, Eglington River Valley) was the random effect, while the cover of *L. polyphyllus* was the fixed effect. The ratios between the numbers of native / alien species were used as the response variable in this model in order to reflect the autocorrelation between the alien and native species richness, recorded on a single vegetation plot.

I tested the significance of particular terms via deletion tests, when the growth of unexplained variance following the removal of a particular term (main effect or interaction) was tested using F-tests in case of regression models and Chi² tests in case of the mixed - effect models. I performed all univariate analyses in R software (R Development Core Team, 2011).

I performed a direct gradient analysis (CCA) to detect the response of community's species composition to the abundance (cover) of *L. polyphyllus*. Before doing the direct gradient analyses, I performed an indirect gradient analysis (DCA) to check for the heterogeneity within the dataset and to decide whether to use a linear or unimodal approximations (Ter Braak and Šmilauer 1998). I used the percentages of species' covers as importance values and included only herbal species and woody juveniles into

all models (both univariate and multivariate), since I did not consider tall woody species likely to be impacted by the dominance of lupins, which I also excluded from all the analyses. I performed all of the multivariate ordination analyses in the CANOCO software (Ter Braak and Šmilauer 1998). I standardized the nomenclature according to Kubát et al. 2002 (Czech Republic), Wilson 1996 (New Zealand) and Turner & Gustafson 2006 (Pacific Northwest, USA).

Results

In all of the three ranges (USA, Czech Republic, New Zealand), I sampled plots with the cover of *L. polyphyllus* of up to 90% (Appendix II).

In the native range (Pacific NW USA), I recorded 112 native species and 52 aliens of European origin exclusively in the vegetation with *L. polyphyllus*. In the Czech Republic, 120 native species were recored in the vegetation invaded by *L. polyphyllus* along with 6 aliens, with origins in Europe or SW Asia. In New Zealand, I recorded only 33 native species within the stands of *L. polyphyllus*, but also 52 alien species, exclusively of european origin (Appendix I and II).

In the Czech Republic, native species' richness responded to the cover of *L. polyphyllus* negativelly (r = -0.294 -Table 1, Fig 1), but the relationship was only marginally significant (p = 0.065 -Table 1, Fig 1). In New Zealand, native species responded to the cover of *L. polyphyllus* negativelly (r = -0.757, p < 0.001 Table 1, Fig. 1). Species of european origin growing as aliens in New Zealand did not respond to the cover of *L. polyphyllus* (r = -0.160, p = 0.324 -Table 1), nor did species native to New Zealand respond to the cover of other invaders of the target communities (*Hieracium pillosella* agg. – r = -0.104, p = 0.523, *Anthoxantum odoratum* – r = 0.070, p = 0.666 -Table 1). I detected no relation between species richness and the cover of *L. polyphyllus* in its native range, Pacific Northwest, USA (r = 0.308, p = 0.163 -Table 1).

Predictor	Response variable	Correlation coefficient	P – value
cover of <i>L. polyphyllus</i>	native species in its native range (NW USA)	0.308	0.163
cover of <i>L. polyphyllus</i>	native species in the Czech Republic (central Europe)	-0.294	0.065
cover of <i>L. polyphyllus</i>	native species in New Zealand	-0.757	< 0.001
cover of <i>L. polyphyllus</i>	alien species (of European origin) in New Zealand	-0.160	0.324
cover of <i>Hieracium pilosella</i> agg.	native species in New Zealand	-0.104	0.523
cover of Anthoxantum odoratum	native species in New Zealand	0.070	0.666

Table I. Response of species richness to the cover of dominant. Only species native to New Zealand revealed a significantly negative response to the cover of the alien *L. polyphyllus*. The response of native species in Europe was negative, but only marginally significant.

The response of species richness to the cover of *L. polyphyllus* differed between the native and invaded ranges (p < 0.001, Chi = 32.15, DF = 2 / 94). In New Zealand, the ratios between the native / alien (of european origin) species richness responded to the cover of *L. polyphyllus* negativelly (p = < 0.001, Chi = 23.547, DF = 1 / 36), indicating that alien species were more successful in the heavily invaded stands compared to native species.

The cover of *L. polyphyllus* proved to be a significant predictor of species composition in all ranges (USA: p = 0.0220; Czech Republic: p = 0.0460; New Zealand: p = 0.0200 - Table 2).

In the USA (native range – Fig. 3) and Czech Republic (Fig. 4), some native species revealed negative response to the cover of *L. polyphyllus*, while others were more



Figure 1. Relation between richness of native species (vertical axis) and cover of *L. polyphyllus* (horizontal axis) in all of the three ranges (USA, Czech Republic, New Zealand). Species richness is expressed as ratios between the richness in a particular plot and maximum richness recorded in the sampled invaded plots in that particular range. Richness of native species on New Zealand reveals a negative relation to the cover of the alien *L. polyphyllus* (full line, y = 0.783 - 0.074x, $R^2 = 0.573$) with the most invaded plots (90% of cover of *L. polyphyllus*, n = 7) harbouring on average only 4.8% of native species richness found in the most diverse plot sampled on New Zealand. Native species in the Czech Republic revealed negative relation to the cover of the alien *L. polyphyllus* (dashed line, y = 0.644 - 0.017x, $R^2 = 0.087$), but the relation was only marginally significant (p = 0.065, t = -1.8972, cor = -0.294, df = 1/38). In the native range of *L. polyphyllus* (dotted line).

Table 2. The cover of *L. polyphyllus* as a predictor of species composition. The table shows results of ordination models, where the cover of *L. polyphyllus* was a predictor variable, while abundances of recorded species were the response variables. In all three ranges, the cover of *L. polyphyllus* was found out to be a significant predictor of species composition – communities with low cover of *L. polyphyllus* qualitatively differed from those with large covers of *L. polyphyllus*.

Range	F-ratio	p-value	Trace
Native range (USA)	1.462	0.022	0.293
Invaded range (New Zealand)	1.597	0.02	0.21
Invaded range (Czech Republic)	1.404	0.046	0.18



Figure 2. Relation between the ratios of native / alien species richness and the cover of *L. polyphyllus*, as recored in New Zealand. A negative response (y = 0.503 - 0.049x, $R^2 = 0.445$) shows that native species were much less successful in the stands with high cover of *L. polyphyllus* compared to aliens, all of which were of European origin.

abundant in plots with high cover of it. Contrary to this, all species native to New Zealand (Fig. 5) revealed negative response to the cover of the alien *L. polyphyllus*, with the exception of *Muehlenbeckia axillaris*, which actually revealed a slight preference for the invaded stands.

Discussion

All these results need to be interpreted with caution, mainly given by the comparative way the data were sampled. It is possible that the factor of the alien's dominance is confounded with other environmental factors, such as anthropogenic disturbance or increased nutrient levels, which may suppress native species and enhance the alien's dominance. It is not really possible to say if the invasion (expressed as the alien's dominance on a given small spatial scale in this study) is promoted by these changes, or if the alien species transforms the sites actively. Alien invasive species have been documented to change site conditions massively, mainly due to substrate stabilisation (L. polyphyllus - Holdaway and Sparrow 2006), litter accumulation (Fraxinus uhdei - Rothstein et al. 2004), nutrient uptake efficiency (Acacia saligna - Odat et al. 2011), water uptake efficiency (Tamarix sp. div. - Di Tomaso 1998) or light deficiency (Cinchona pubescens - Järger et al. 2007). Therefore, it is difficult to say in which way the causality between the occurrence of aliens and altered site conditions goes – does L. polyphyllus alter the site conditions by itself, due to nitrification, substrate stabilisation and limited insolation, or does it just benefit from human-induced ruderalization? Both of these mechanisms are likely to work in concert, and either of them can prevail in a particular situation. This makes it very difficult to find a general answer to the question of the



Figure 3. Ordination diagram (CCA) showing the response of species composition to the cover of *L. polyphyllus* in its native range, USA. The first ordination axis (constrained or canonical axis) represents the predictor variable – the cover of *L. polyphyllus*. Native species like *Potentilla gracilis* or *Epilobium ciliatum* reveal negative response to the cover of *L. polyphyllus*, while others, like *Anaphallis margaritacea*, reveal a positive response. The second axis is unconstrained and represents some other environmental gradient, which is difficult to interpret in this case.

agrcap = Agrostis capillaris, agrrep = Agropyron repens, alopra = Alopecurus pratensis, anamar = Anaphallis margaritacea, astsub = Aster subspicatus, caraur = Carex aurea, colpar = Collinsia parviflora, crebie = Crepis biennis, desces = Deschampsia cespitosa, epicil = Epilobium ciliatum, equarv = Equisetum arvense, fespra = Festuca pratensis, hiecyn = Hieracium cynoglossoides,hollan = Holcus lanatus, hypper = Hypericum perforatum, junbal = Juncus balticus, junxip = Juncus xiphioides, lyceur = Lycopus europaeus, phlpra = Phleum pratense, potgra = Potentilla gracilis, pteaqu = Pteridium aquilinum, rosgym = Rosa gymnocarpa, rumace = Rumex acetosa, rubide = Rubus idaeus, stegra = Stellaria graminea, Sisyrrhynchium idahoense, taroff = Taraxacum officinale, tribor = Trientalis borealis

direction of causality between the invasions by alien plants and changes of site conditions, leading to changes in diversity and composition. The period a particular site has been invaded brings another interpretation difficulty – milder impact of the alien can be caused by the site's having been invaded recently and vice versa. On the other



Figure 4. Ordination diagram (CCA) showing the response of species composition to the cover of L. polyphyllus in the Czech Republic. The first ordination axis (constrained or canonical axis) represents the predictor variable – the cover of L. polyphyllus. Same as in its native range, USA, some native species (Myosoton aquaticum, Stellaria nemorum, Bistorta major) reveal a positive relation to the cover of L. polyphyllus, while others (Festuca rubra) reveal a strongly negative relation. The second axis is unconstrained and very likely represents some environmental gradient related to moisture, with species like Hypericum perforatum, Festuca rubra and Plantago lanceolata in the lower part and *Phalaris arundinacea* and *Cirsium oleraceum* in the upper part of the diagram. acocal = Aconitum callibotryon, agrcap = Agrostis capillaris, alcvul = Alchemilla vulgaris agg., alopra = Alopecurus pratensis, bismaj = Bistorta major, chahir = Chaerophyllum hirsutum, cirarv = Cirsium arvense, cirole = Cirsium oleraceum, crulae = Cruciata laevipes, dacglo = Dactylis glomerata, epiang = Epilobium angustifolium, fespra = Festuca pratensis, fesrub = Festuca rubra, filulm = Filipendula ulmaria, galapa = Galium aparine, galmol = Galium mollugo, galpub = Galeopsis pubescens, hersph = Heracleum sphondilium, hypmac = Hypericum maculatum, hypper = hypericum perforatum, myoaqu = Myosoton aquaticum, phaaru = Phalaris arundinacea, plalan = plantago lanceolata, ranrep = Ranucnulus repens, sanoff = Sanguisorba officinalis, senfuc = Senecio fuchsi agg., stenem = Stellaria nemorum, trifla = Trisetum flavescens, trirep = Trifolium repens, urtdio = Urtica dioica, vercha = Veronica chamaedrys, viccra = Vicia cracca

hand, this factor can be presumed to play only a marginal role in regularly disturbed communities, where the succession series is blocked by flooding, grazing or mowing.

Be that as it may, the results show that in the invaded ranges, the dominance of *L. polyphyllus* is associated with site conditions that do not favor native species,



Figure 5. Ordination diagram (CCA) showing the response of species composition to the cover of *L. polyphyllus* in New Zealand. The first ordination axis is constrained and represents the predictor variable – the cover of *L. polyphyllus*.

All species native to New Zealand revealed a negative relation (*Discaria toumatou, Acaena inermis, Gonocarpus aggregatus, Rhytidosperma gracilis*), with the exception of *Muehlenbeckia axillaris*, which reveals a positive relation to the cover of *L. polyphyllus*. The second ordination axis (vertical) is unconstrained and difficult to interpret in this case. *acaine = Acaena inermis, achmil = Achillea millefolium* agg., *agrsto = Agrostis stolonifera, aircar = Aira caryophyllea, antodo = Anthoxantum odoratum, arreal = Arrhenatherum elatius, avefat = Avenula fatua, blemon = Blechnum montanum, blepen = Blechnum penna – marina, cerhol = Cerastium holosteoides, cirarv = Cirsium arvense, cirvul = Cirsium vulgare, corsar = Coriaria sarmentosa, crecap = - Crepis capillaris, desces = Deschampsia cespitosa, distou = Discaria toumatou, fesaru = Festuca arundinacea, fesovi = Festuca ovina, gonocr = Gonocarpus aggregatus, hiepil = Hieracium pilosella* agg., *hollan = Holcus lanatus, luzcam = Luzula campestris, mueaxi = Muehlenbeckia axillaris, phypus = Phymatosorus pustulatus, poapra = Poa pratensis, poatri = Poa trivialis, rhygra = Rhytidosperma gracilis, sagpro = Sagina procumbens, senjac = Senecio jacobaea, tricam = Trifolium campestre, trihyb = Trifolium hybridum*

which is especially apparent in New Zealand. Contrary to that, species from the native range were successful when growing with *L. polyphyllus*, more than species from both invaded ranges (Czech Republic and New Zealand). This is likely to be due to these species' being well apapted to the conditions of sites distinctively dominated by *L. polyphyllus*, which may be caused by the long-term coevolution of communities and species' filtering in the dominant species' native range. Due to the long-term presence of the dominant species *L. polyphyllus*, species in the native range have been selected to coexist with it, otherwise they would have been eliminated from communities where *L. polyphyllus* is a dominant species.

Contrary to that, L. polyphyllus is a newly imported dominant species to the communities in the invaded ranges. In Europe, the invasion of L. polyphyllus is associated with some loss of native species richness (see for example Valtonen et al. 2006), but around 70% of present species are capable of growing in dense stands of this alien, as documented earlier by Hejda et al. (2009). Obviously, most of the species in the invaded communities in the Czech Republic are strong competitors that are not easily supressed by the alien L. polyphyllus and majority of them can thrive even in the stands with a high cover of *L. polyphyllus*. This ability may have evolved as a result of longterm presence of distinctive dominant species native to the Czech Republic, such as Aegopodium podagraria, Cirsium heterophyllum, Dactylis glomerata, Senecio hercynicus or Trisetum flavescens (see primary data in Appendix II). In other words, the long-term evolution of these communities have resulted in a state, when only species that successfuly compete with native dominants are present. In Europe, many native species utilize a similar niche as invasive aliens and prefer human disturbed places, or, on the contrary, places where the regular disturbance or management regime has ceased (Hobbs and Huenneke 1992, Davis and Pelsor 2001). In these communities, the competitive effect of the alien L. polyphyllus may not differ substantially from competitive effects of native dominants.

Species native to New Zealand were found to be least successful when growing in the stands of *L. polyphyllus* in this study, with the most invaded plots (with the cover of L. polyphyllus of 90%) being almost free of species native to New Zealand. This can be partly related to the fact that, in New Zealand, L. polyphyllus often invades relatively unstable and regularly disturbed riparian terraces where the vegetation is not really dense, so the level of interspecific competition can be expected to be low. Therefore, heliophilous species of these communities (Coriaria plumosa, Epilobium melanocaulon, Parahebe decora, Raoullia subsericera, R. hookeri, Wahlenbergia albomarginata) are weak competitors when confronted with the distinctive alien dominant and this can be caused mainly by the differences in the type of invaded habitats between these two distinct invaded ranges (Czech Republic and New Zealand). On the other hand, L. polyphyllus also invades more stable and less frequently disturbed riparian meadows in New Zealand, with species like Acaena inermis, Carex geminata, Gonocarpus aggregatus or Prasophyllum colensoi on wet places and Brachyglottis bellidioides, Celmisia gracillenta, Discaria toumatou or Leucopogon fraseri on dryer sites. In these communities, the vegetation is dense and the level of interspecific competition can be expected to be rather high, but native species still fail to coexist with the dominant invasive alien L. polyphyllus. It is possible that the intensity of interspecific competition is generally lower in the communities of New Zealand and native species are weaker competitors due to, for example, the effects of insularity, which means a long-term isolated development and not having been confronted with competitively strong species with cosmopolitan tendencies. At the same time, the insular flora of New Zealand can

be expected to be phylogenetically rather homogenous, originating from a few clades originally colonizing the islands. Such communities have been documented to be more easily invaded (Gerhold et al. 2011). The habitat-based and geography-based explanations of the low abilities of species native to New Zealand to thrive within the stands of *L. polyphyllus* are definitelly not exclusive and it is very likely that they work together. The only species native to New Zealand that revealed a positive relation to the cover of the alien *L. polyphyllus* was *Muehlenbeckia axillaris*, as shown by the multivariate ordination analysis – Fig. 5.

In New Zealand, *L. polyphyllus* has been documented to accumulate silt material and therefore accelerate the stabilization of riparian terraces (Holdaway and Sparrow 2006). This effect may facilitate the site for some species, a similar pattern was observed in the native range, where a related species *L. lepidus* was observed to accelerate the succession by remediating site conditions on pumice fields, which are unstable and experience periods of thermic and hydric stress during the vegetation season (Del Moral and Rozzell 2005). A similar principle can be expected to work on the unstable riparian terraces in New Zealand, but this process is more likely to promote aliens of European origin rather than competitivelly weak species native to New Zealand.

The target communities in New Zealand were also heavilly invaded by other aliens, like *Anthoxantum odoratum* and *Hieracium pilosella* agg., so the potential impact of the invasive alien *L. polyphyllus* was heavily confounded with possible impacts of other invasive species. *Anthoxantum odoratum* forms dense and homogenous stands, while *H. pilosella* agg. forms dense 'pillows' of leaf rosettes. But richness of species native to New Zealand was not found to be related to the cover of either of these aliens of european origin, when sampled and tested in the same way as the relation to the cover of *L. polyphyllus*. Some native species, like *Brachyglottis bellidioides, Coprosma atropurpurea* or *Celmisia gracillenta* were actually found to prefer places with large covers of *H. pilosella*'s rosettes. For these reasons, it is highly likely that the site conditions that depauperate the diversity of communities in New Zealand are associated with the invasion by *L. polyphyllus*, rather than with other abundant aliens, such as *Anthoxantum odoratum* and *Hieracium pilosella* agg.

The data shows that species in the native range are able to coexist with the dominant lupins better than species from the invaded ranges. Out of the two invaded ranges studied, species native to New Zealand were found to be most effectively eliminated from communities dominated by the alien *L. polyphyllus*. An uncertainty remains whether this effect is caused by the invading *L. polyphyllus* or by other environmental factors that promote the invasion, such as human induced disturbance, nitrification or substrate stabilisation, however, some of these changes can be promoted by the invasion by *L. polyphyllus* too. Even though it is difficult to separate causes and effects of the invasion in this case (as it is with most invasions), the results show that different native species respond differently to the invasion by a single alien. In one invaded range – Europe, most species are able to coexist with the invasive *L. polyphyllus*, while in New Zealand, native species are virtually eliminated from stands with a high cover of the dominant alien *L. polyphyllus*. It remains questionable to which degree the results scale up from tiny vegetation plots to larger units in New Zealand. The results show that at the fine scale, the invasion is associated with a severe degradation of communities, so it is likely that its potential impacts are apparent even at larger scales, due to, for example, reduction of populations of native species. In the extreme cases, this can lead to local extinctions in areas with large stands of *L. polyphyllus*, such as the valley of Waimakariri river in the Arthur Pass National Park, NZ. Moreover, this alien invades pristine areas with many rare species and its invasion therefore represents a serious threat to native plant diversity at the fine scale and a threat to landscape character at larger scales. High local abundances observed in the invaded ranges suggest that *L. polyphyllus* has the potential to spread further, well beyond the boundaries of its current distribution.

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References

- Aniszewski T (1993) Nutritive Quality of the Alkaloid Poor Washington Lupin (*Lupinus poly-phyllus*) Lindl var SF TA as a Potentional Protein Crop. Journal of the Science of Food and Agriculture 61 (4): 409–421. doi: 10.1002/jsfa.2740610406
- Crawley MJ (2007) The "R" Book. John Wiley & Sons Ltd., Chichester, West Sussex, England. 942 p. doi: 10.1002/9780470515075
- Davis MA (2003) Biotic globalization: Does competition from introduced species threaten biodiversity? Bioscience 53 (5): 481–489. doi: 10.1641/0006-3568(2003)053[0481:BGD-CFI]2.0.CO;2
- Davis MA, Pelsor M (2001) Experimental support for a resource-based mechanistic model of invasibility. Ecology Letters 4 (5): 421–428. doi: 10.1046/j.1461-0248.2001.00246.x
- del Moral R, Rozzell LR (2005) Long-term effects of *Lupinus lepidus* on vegetation dynamics at Mount St. Helens. Plant Ecology 181 (2) 203–215. doi: 10.1007/s11258-005-6627-4
- Di Tomaso JM (1998) Impact, biology, and ecology of Saltcedar (*Tamarix* spp.) in the Southwestern United States. Weed Technology 12: 326–336. IDS Number: 104GE, ISSN: 0890-037X
- Gerhold P, Partel M, Tackenberg O, Hennekens SM, Bartish I, Schaminee JHJ, Fergus AJF, Ozinga WA, Prinzing A (2011) Phylogenetically Poor Plant Communities Receive More

Alien Species, Which More Easily Coexist with Natives. Američan Naturalist 177 (5): 668–680. doi: 10.1086/659059

- Hejda M, Pyšek P, Jarošík V (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. Journal of Ecology 97: 393–403. doi: 10.1111/j.1365-2745.2009.01480.x
- Hobbs RJ, Huenneke LF (1992) Disturbance, Diversity, and Invasion: Implications for Conservation. – Conservation Biology 6 (3): 324–337. doi: 10.1046/j.1523-1739.1992.06030324.x
- Holdaway RJ, Sparrow AD (2006) Assembly rules operating along a primary riverbed-grassland successional sequence. Journal of Ecology 94: 1092–1102. doi: 10.1111/j.1365-2745.2006.01170.x
- Järger H, Tye A, Kowarik I (2007) Tree invasion in naturally treeless environments: Impacts of quinine (*Cinchona pubescens*) trees on native vegetation in Galápagos. Biological Conservation 140: 297–307. doi: 10.1016/j.biocon.2007.08.014
- Kubát K, Hrouda L, Chrtek J jun., Kaplan Z, Kirschner J, Štěpánek J (Eds) (2002) Key to the Flora of the Czech Republic. Academia, Prague.
- Lye GC, Kaden JC, Park KJ (2010) Forage use and niche partitioning by non-native bumblebees in New Zealand: implications for the conservation of their populations of origin. Journal of Insect Conservation 14: 607–615. doi: 10.1007/s10841-010-9287-1
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: Causes, epidemiology, global consequences, and control. Ecological Applications 10 (3): 689–710. doi: 10.2307/2641039
- Manchester SJ, Bullock JM (2000) The impacts of non-native species on UK biodiversity and the effectiveness of control. Journal of Applied Ecology 37 (5): 845–864. doi: 10.1046/j.1365-2664.2000.00538.x
- Mason TJ, French K (2008) Impacts of a woody invader vary in different vegetation communities. Diversity and Distributions 14: 829–838. doi: 10.1111/j.1472-4642.2008.00493.x
- Odat N, Al Khateeb W, Muhaidat R, Al'udatt M, Irshiad L (2011) The effect of exotic *Acacia saligna* tree on plant biodiversity of Northern Jordan. International Journal of Agriculture and Biology 13: 823–826. IDS Number: 835VB ISSN: 1560-8530.
- Payne WA, Chen C, Ball DA (2004) Agronomic potential of narrow-leafed and white lupins in the inland Pacific Northwest. Agronomy Journal 96 (6): 1501–1508. IDS Number: 876YV ISSN: 0002-1962
- R Development Core Team (2011) R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. ISBN 3-900051-07-0, URL http://www.R-project.org/.
- Rothstein DE, Vitousek PM, Simmons BL (2004) An exotic tree alters decomposition and nutrient cycling in a Hawaiian montane forest. Ecosystems 7: 805–814. doi: 10.1007/ s10021-004-0009-y
- Scott D (2007) Sustainability of high-country pastures under contrasting development inputs.
 9. Vegetation dynamics. New Zeal Journal of Agricultural Research 50 (3): 393–406. IDS Number: 224VI ISSN: 0028-8233
- Slavík B, Hejný S, Chrtek J jun., Tomšovic P (Eds) (1997) Flora of the Czech Republic 5th. edn. - Academia, Praha

- Stout JC, Kells AR, Goulson D (2002) Pollination of the invasive exotic shrub Lupinus arboreus (Fabaceae) by introduced bees in Tasmania. Biological Conservation 106: 425–434. doi: 10.1016/S0006-3207(02)00046-0
- Ter Braak CJF, Šmilauer P (1998) CANOCO Reference Manual and User's Guide to Canoco for Windows – Software for Canonical Community Ordination 4th. edn. - Wageningen, Netherlands: Centre for Biometry.
- Tilman D (1999) The ecological consequences of changes in biodiversity: A search for general principles. Ecology 80 (5): 1455–1474. doi: 10.1890/0012-9658(1999)080[1455:TECO-CI]2.0.CO;2
- Turner M, Gustafson P (2006) Wildflowers of the Pacific Northwest. Timber Press, Portland, Oregon , USA.
- Valtonen A, Jantunen J, Saarinen K (2006) Flora and lepidoptera fauna adversely affected by invasive *Lupinus polyphyllus* along road verges. Biological Conservation 133: 389–396. doi: 10.1016/j.biocon.2006.06.015
- Vilà M, Basnou C, Pyšek P, Josefsson M, Genovesi P, Gollasch S, Nentwig W, Olenin S, Roques A, Roy D, Hulme PE, DAISIE partners (2010) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. Frontiers in Ecology and The Environment 8 (3): 135–144. doi: 10.1890/080083
- Wilson HD (1996) Wild Plants of Mt. Cook National Park. Manuka Press, Christchurch, New Zealand

Appendix I

Entry data for the univariate models with species richness as a response variable. (doi: 10.3897/neobiota.17.4317.app1) File format: Micrisoft Excell document (xls).

Explanation note: The file presents the entry data for i) the mixed effect model testing the differences between all three ranges and ii) data with native / alien species richness ratios used for testing the response of native species versus aliens of european origin on New Zealand.

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Citation: Hejda M (2013) Do species differ in their ability to coexist with the dominant alien *Lupinus polyphyllus*? A comparison between two distinct invaded ranges and a native range. NeoBiota 17: 39–55. doi: 10.3897/neobiota.17.4317 Entry data for the univariate models with species richness as a response variable. doi: 10.3897/neobiota.17.4317.app1

Appendix 2

Raw data on species composition and abundances, expressed as the percentage covers of recorded species. (doi: 10.3897/neobiota.17.4317.app2) File format: Micrisoft Excell document (xls).

Explanation note: The data with species composition were used for the multivariate ordination models, testing the response of individual species to the gradient of the cover of *L. polyphyllus*.

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RESEARCH ARTICLE



The role of eco-evolutionary experience in invasion success

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Abstract

Invasion ecology has made considerable progress in identifying specific mechanisms that potentially determine success and failure of biological invasions. Increasingly, efforts are being made to interrelate or even synthesize the growing number of hypotheses in order to gain a more comprehensive and integrative understanding of invasions. We argue that adopting an eco-evolutionary perspective on invasions is a promising approach to achieve such integration. It emphasizes the evolutionary antecedents of invasions, i.e. the species' evolutionary legacy and its role in shaping novel biotic interactions that arise due to invasions. We present a conceptual framework consisting of five hypothetical scenarios about the influence of so-called 'eco-evolutionary experience' in resident native and invading non-native species on invasion success, depending on the type of ecological interaction (predation, competition, mutualism, and commensalism). We show that several major ecological invasion hypotheses, including 'enemy release', 'EICA', 'novel weapons', 'naïve prey', 'new associations', 'missed mutualisms' and 'Darwin's naturalization hypothesis' can be integrated into this framework by uncovering their shared implicit reference to the concept of eco-evolutionary experience. We draft a routine for the assessment of eco-evolutionary experience in native and non-native species using a food web-based example and propose two indices (xp Enert index and xp_{Residents} index) for the actual quantification of eco-evolutionary experience. Our study emphasizes the explanatory potential of an eco-evolutionary perspective on biological invasions.

Keywords

Alien species, ecological novelty, ecological similarity, introduced species, invasibility, invasiveness, naïveté, non-indigenous species

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Making the case for an eco-evolutionary perspective on biological invasions

A large number of hypotheses about the mechanisms that determine the success or failure of biological invasions have been proposed (reviews in Inderjit et al. 2005, Hufbauer and Torchin 2007, Catford et al. 2009, Jeschke et al. 2012). However, most of these hypotheses are restricted to specific processes (e.g. enemy release hypothesis, Keane and Crawley 2002, or novel weapons hypothesis, Callaway and Aschehoug 2000) and do not explain variation in invasion success on a more inclusive level. Thus, despite considerable progress in invasion ecology, the search for a more comprehensive and integrative understanding of biological invasions is still on-going (Davis 2009, Richardson 2011, Heger et al. in press). Accordingly, increasing efforts are being made to interconnect or even synthesize the growing number of hypotheses and concepts (e.g. Catford et al. 2009, Blackburn et al. 2011, Gurevitch et al. 2011).

With this conceptual paper we aim at contributing to this important development. We suggest that adopting an eco-evolutionary perspective on invasions is a promising approach to achieve a broader conceptual synthesis in invasion ecology (cf. Heger et al. 2013). Scientific awareness of evolutionary aspects in biological invasions has increased in the last decade (Sax and Brown 2000, Sakai et al. 2001, Hänfling and Kollmann 2002, Lee 2002, Sax et al. 2005, 2007, Facon et al. 2006, Kondoh 2006, Hufbauer and Torchin 2007). But the focus of most studies in this field lies particularly on the evolutionary consequences of invasions, i.e. the evolutionary response of species to invasions (see e.g. Cox 2004, Strayer et al. 2006, Carlsson et al. 2009, Orians and Ward 2010). Our focus, on the contrary, lies on elucidating the role that evolutionary antecedents may play for invasion success (see e.g. Cox and Lima 2006, Kondoh 2006, Mitchell et al. 2006, Sih et al. 2010, Thuiller et al. 2010). It is a general presumption in ecology that biotic interactions are influenced by the evolutionary legacy of the interacting species (Pianka 2000). During invasions, species reach areas where they are not native and interact with species that they have not evolved with (Heger and Trepl 2003, Cox 2004). Such settings lead to 'novelty' in biotic interactions in invaded areas, which may likely be decisive for the success or failure of invasions. In the following, we show on theoretical grounds that adopting an eco-evolutionary perspective on invasions (i) offers the possibility to consider the roles that both native *and* non-native species play in invasion success or failure, i.e. species invasiveness and community invasibility; (ii) allows an integrative and at the same time differentiated treatment of invasions that affect different types of ecological interaction (competition, predation, mutualism, commensalism); and (iii) has the potential to link so far apparently disconnected major invasion hypotheses in one common framework.

A framework for explaining variation in invasion success based on the concept of eco-evolutionary experience

During evolution, species adapt to biotic interactions in their native environment. They thereby accumulate what we propose to term 'eco-evolutionary experience' in dealing with these interactions. We hypothesize that this inherited experience – possibly complemented by experience acquired during an individual's lifetime (e.g. predators getting better at capturing prey during successive encounters) - ultimately determines the species' proficiency to survive and prosper within new ecological contexts, as for example when invasions take place. For an introduced species, the biotic community in its exotic range may differ fundamentally from the one in its native environment. Biotic interactions that evolutionarily shaped the introduced species in its native environment may become interrupted (Mitchell et al. 2006). At the same time, the resident organisms in the exotic range are confronted with a species they have never met before. For instance, native prey species may not be familiar with the hunting strategy of a non-native predator, and at the same time the latter may be unprepared for having to compete for prey with other (resident) predators. Thus, as a consequence of biological invasions, biotic interactions arise that may be novel to both introduced and native species. Both sides then depend on their inherited eco-evolutionary experience to react appropriately to the new situation. Plasticity (e.g. in behaviour or morphology) resulting from adaptation to unstable environmental conditions in previous times may play an important role here (Nussey et al. 2005, Richards et al. 2006, Sol et al. 2008, Engel et al. 2011). The degree of eco-evolutionary experience available on either side may thus also be interpreted in terms of the introduced species' invasiveness and the native community's invasibility, respectively.

Figure 1 illustrates a conceptual framework to explain variation in invasion success based on the concept of eco-evolutionary experience. The framework consists of five hypothetical scenarios, corresponding to five major types of ecological interaction: the introduced species acting as prey (Fig. 1A), predator (including herbivores, parasites, and parasitoids; Fig. 1B), competitor (Fig. 1C), mutualist (Fig. 1D) or commensal (Fig. 1E). The graphs presented in each scenario are speculative, their exact shape still to be substantiated with empirical data in future studies. However, the scenarios formulate our generalized hypotheses about the relationship between the eco-evolutionary experience in the interacting introduced and native species on the one hand and the relative probability of the respective invasion to succeed on the other: For predator-prey and competitive interactions, the probability of a successful invasion is likely to be higher with a low degree of applicable eco-evolutionary experience in the native species and a high degree in the non-native species (Fig. 1A, B, C). Widely known examples where these circumstances likely apply include the invasion of purple loosestrife (Lythrum salicaria) in North America where it lacks herbivorous enemies that feed on it in its native range (Blossey and Nötzold 1995, Fig. 1A), mammalian invasions on oceanic islands causing the extinction of naïve local avifauna (Blackburn et al. 2004, Fig. 1B), and introduced diffuse knapweed (Centaurea diffusa) having allelopathic effects on competing resident native grass species in North America (Callaway and Aschehoug 2000, Fig. 1C). In mutualistic interactions, a high degree of experience in both the non-native and the native mutualist is likely to be advantageous for invasion success (Fig. 1D). This may be the case e.g. for yellow crazy ants (Anoplolepis gracilipes) associating with honeydew-producing hemipteran insects on Christmas Island



Figure 1. Framework of five hypothetical scenarios about the influence of eco-evolutionary experience in the non-native (dashed line) and native species (solid line) on the relative probability of invasion success, according to the type of ecological interaction (A/B: predator-prey, C: competition, D: mutualism, E: commensalism). In general, lower native experience (except in mutualistic interactions) and higher non-native experience is likely to be advantageous for invasion success. Shaded ovals exemplarily indicate parts of the framework covered by major hypotheses in invasion ecology that implicitly share a reference to the importance of evolutionary legacy for invasion success (see main text and Appendix I for details and references).

(O'Dowd et al. 2003, see also Styrsky and Eubanks 2007). In commensal interactions, eco-evolutionary experience may only have an influence on invasion success if the non-native species is the benefiting commensal (Fig. 1E). In such cases, a higher non-native experience for taking advantage of the native host should be favourable, while the experience level of native hosts is irrelevant, since *per definitionem* the host is not affected by the commensal. This may be the case e.g. for human affiliates like house sparrows (*Passer domesticus*) that successfully invade new areas by being able to reach high population densities in human settlements (cf. Jeschke and Strayer 2006). In the case of a native commensal (not shown in Fig. 1), experience on neither side should have an effect on invasion success, because the non-native host remains unaffected, and the facilitation of the native commensal does not necessarily bear on invasion success.

Notably, several major invasion hypotheses can be integrated into this framework. From an eco-evolutionary viewpoint, it becomes apparent that they actually share an implicit reference to the role of evolutionary legacy in invasion success. This includes such often-cited hypotheses as 'enemy release' (Keane and Crawley 2002), 'evolution of increased competitive ability' (EICA; Blossey and Nötzold 1995), 'novel weapons' (Callaway and Aschehoug 2000) and 'Darwin's naturalization hypothesis' (Daehler 2001, Procheş et al. 2008, Thuiller et al. 2010). Further examples are the hypotheses of 'new associations' (Hokkanen and Pimentel 1989, Mitchell et al. 2006), 'naïve prey' (Cox and Lima 2006), 'missed mutualisms' (Alpert 2006), 'mutualist facilitation' (Richardson et al. 2000), and 'human commensals and imperialism' (Jeschke and Strayer 2006). Most of the invasion examples given in the previous paragraph directly apply to one of these hypotheses. Appendix I provides examples of how the central reasoning of the hypotheses can be related to the concept of eco-evolutionary experience, which is visualized correspondingly in Fig. 1 by shaded ovals. Despite this implicit relatedness, they are usually considered separately, sometimes even as mutually exclusive. Only few studies consider potential interrelations between the hypotheses (but see Inderjit et al. 2005, Hufbauer and Torchin 2007, Sih et al. 2010, Gurevitch et al. 2011).

By adopting an explicit eco-evolutionary perspective, the framework provides a basis for interrelating the hypotheses (as defined in Appendix I) and conclusions based on them, but it also highlights their shortcomings: the hypotheses of enemy release, EICA, Darwin's naturalization hypothesis, naïve prey and novel weapons consider the degree of experience only on the native species' side (Appendix I: a, b, d, e, f), while new associations, missed mutualisms, and the human commensals and imperialism hypothesis focus on the non-natives' experience (Appendix I: c, g, i). Only the mutualist facilitation hypothesis at least implicitly considers both sides (Appendix I: h). Thus, these invasion hypotheses emphasize either the invasibility of native communities or the invasiveness of non-native species and neglect that the outcome of an invasion is probably influenced by the degree of applicable eco-evolutionary experience on both interacting sides (cf. Sih et al. 2010). The framework presented here provides a basis for considering both sides simultaneously in order to achieve a more comprehensive understanding of variation in invasion success.

Quantifying eco-evolutionary experience: a food web-based example

Clearly, in connection with the framework presented here, practicable approaches to actually quantify eco-evolutionary experience are needed. Such approaches can build on the general assumption that more of the eco-evolutionary experience in species (native or introduced) will be applicable to a new interaction setting if that setting is ecologically similar to previous interactions. In other words, the degree of ecological similarity between new and previous interaction settings may be taken as a proxy for the degree of applicable eco-evolutionary experience in native and non-native species.

Ecological similarity of species is often assumed to be positively correlated with the taxonomic or phylogenetic relatedness between them (e.g. Agrawal and Kotanen 2003, Ricciardi and Atkinson 2004, Cavender-Bares et al. 2004, Strauss et al. 2006, Diez

et al. 2008, Procheş et al. 2008). Although convenient, this approach has important limitations. In particular, similarity – be it in respect to morphological, behavioural, or ecological traits – does not necessarily correlate with relatedness (Losos 2008, Thuiller et al. 2010). This becomes most evident in cases of convergent evolution where relatively unrelated species show a high degree of similarity (see e.g. Futuyma 2005). Thus, taxonomic classification and phylogenetic relatedness of species are unreliable indicators for their ecological similarity and therefore also for the similarity of biotic interactions of these species before and after an invasion event.

Our approach for quantifying eco-evolutionary experience of introduced and native species assesses the ecological similarity of the ecological interaction settings these species are part of before and after the invasion. Such comparisons can be done for any ecological network, e.g. plant-pollinator networks, seed-dispersal interactions, hostparasite systems or food webs. We here present an example for a quantification routine based on food webs (summarized in Appendix II), which covers predator-prey, competitive, and indirect mutualistic interactions (e.g. a predator and a primary producer indirectly benefitting from each other as the predator feeds on the herbivore that consumes the primary producer). We compare the food webs of the original 'source' area and a new 'target' area of the introduced species (hereafter called the 'focal species') regarding the occurrence and occupancy (in terms of number of species) of ecological guilds. Note that the term 'guild' as we use it here is not restricted to referring exclusively to "a group of species that exploit the same class of environmental resources in a similar way" (Root 1967). We use a broader definition, where guilds can also be, for instance, groups of species that share the same predators or anti-predator strategies. The exact definition should be chosen based on the particular context of a study. Other ecological groupings (e.g. functional groups or types) can be used instead of guilds as well (for more details on ecological groupings, see e.g. Hawkins and MacMahon 1989, Wilson 1999, Blondel 2003, Blaum et al. 2011).

Eco-evolutionary experience of the introduced focal species

In order to assess the experience of the focal species after its introduction to a target area, we compare the interactions in the food webs of these two areas from the perspective of the focal species (steps 1 to 4 in Appendix II). Both food webs will be composed of different trophic levels, each of which may contain species of different ecological guilds. For simplicity, we restrict our analysis to direct interactions and single-step indirect interactions (i.e. including one intermediate species as for example in exploitative competition) of the focal species with resident species (step 1 in Appendix II). These interactions can be assumed to have the most immediate consequences for the invasion success of the focal species. Separately for each type of interaction (i.e. the focal species acting as prey, predator, competitor or indirect mutualist), and for both the source and target area, the respective interaction partners are classified into their ecological guilds and the members of each guild are counted (steps 2 and 3 in Appendix

II). In this way, we obtain datasets for each type of interaction, with species numbers per guild in both the source and target area (see exemplary Table A in Appendix II).

To actually calculate the eco-evolutionary experience of the focal species (step 4 in Appendix II), we need an index of similarity. The Bray-Curtis similarity index (*sbc*) is often used in ecological studies when comparing the species composition of different samples, e.g. community samples:

$$sbc_{jk} = 1 - \frac{\sum_{i=1}^{n} |N_{ij} - N_{ik}|}{\sum_{i=1}^{n} (N_{ij} + N_{ik})}$$
, (Eq. 1)

where *n* is the total number of species considered, and N_{ij} and N_{ik} represent the number of individuals of species *i* in the samples *j* and *k*, respectively. Absolute abundance differences in all species are summed up in the numerator and standardized by the total number of individuals in all species from both samples in the denominator. However, while this index provides some grasp on the absolute difference between the samples, it does not consider the direction of change in numbers. But this is important from an eco-evolutionary perspective in the invasion context: for the focal species, it is decisive whether it encounters more or fewer interaction partners from particular guilds in the target area than in the source area. We thus adapted the Bray-Curtis index to account for this specific need. The new index is an index of experience rather than just similarity. We thus call it ' xp_{Facel} index':

$$xp_{Focal} = 1 - \frac{\sum_{i=1}^{n} \max(0; N_{iT} - N_{iS})}{\sum_{i=1}^{n} (N_{iT} + N_{iS})} , \text{ (Eq. 2)}$$

where *n* is the total number of guilds considered, and N_{iS} and N_{iT} represent the number of species in guild *i* in the source (*S*) and target (*T*) area, respectively, that interact with the focal species. Values of xp_{Focal} range between 0 (no applicable experience in the target area) to 1 (maximum applicable experience). By considering not only the presence or absence of guilds but also how numbers of species occupying these guilds differ between source and target area, the xp_{Focal} index accounts for trait differences on the guild level as well as species level. In contrast to the Bray-Curtis index, however, the xp_{Focal} index only considers those differences in the number of guild members where $N_{iS} < N_{iT}$ by introducing the 'max' term in the numerator. From the perspective of the focal species, these are the relevant differences between the source and target area, because a larger number of interaction partners of a guild in the target area compared to the source area implies a reduced (or even absent) eco-evolutionary experience of the focal species in the new interaction setting.

This is obvious in cases where the focal species meets interaction partners of a guild in the target area that was entirely absent in the source area (i.e. when $N_{is}=0$ and $N_{i7}>0$), being then unable to count on applicable eco-evolutionary experience

for these new interactions. But reduced experience is also expected when the focal species interacts with species even of a familiar guild if they occur in larger numbers in the target area as compared to the source area $(N_{is} < N_{iT})$. This is reasonable to assume because also species of the same guild differ from each other. Although these differences are relatively small (otherwise the species would be classified into different guilds), they can still be relevant for the focal species. Thus, the more interacting species exist in the target area in comparison to the source area (i.e. the larger N_{iT} is in relation to N_{c}), the higher is the probability that the focal species will have to respond to unknown ecological traits, and the lower is its experience in the target area. By contrast, the probability of having to respond to unfamiliar ecological traits of species of a particular guild is low when the focal species has already interacted with a larger number of species from that guild in the source area than in the target area. Our model makes the simplifying assumption of a threshold where the focal species has the maximum eco-evolutionary experience with the new interaction setting $(xp_{Focal}=1)$ when it has interacted with at least as many species in each guild in the source area as it encounters in the target area (i.e. if $N_{is} \ge N_{iT}$). In future studies, alternative formulations without such a threshold may be explored.

To a certain degree, the xp_{Focal} index allows reduced experience with members of a particular guild to be compensated by experience in the same type of interaction with species of other guilds. For instance, in predator-prey interactions the focal species may not be familiar with predators of a particular guild in the target area, but may also not be entirely naïve because of having evolved in its source area in the presence of predators at least from other guilds. However, under the assumptions of the xp_{Focal} index, such 'unspecific' experience with a type of interaction (in this example 'predation') will not completely offset missing experience with a particular guild.

Eco-evolutionary experience of the resident species community

In order to assess the experience of the resident species community facing a new introduced species, we first determine the focal species' guilds for each type of interaction, i.e. when it may act either as a predator, prey, competitor or indirect mutualist. We then count the number of resident species that are already present in these specific guilds in the target area (see step 5 and exemplary Table B in Appendix II). Finally, by calculating the following ' $xp_{Residents}$ index' separately for each type of interaction (step 6 in Appendix II), we can assess, in a first approximation, how much experience native species have with the focal species:

$$xp_{Residents} = 1 - \frac{1}{N_{i^*T} + 1}$$
, (Eq. 3)

where N_{i^*T} is the number of resident species in the same guild (i^*) as the focal species in the respective type of interaction. The fraction in this index provides an

estimate how ecologically 'novel' the focal species is for the resident community. The maximum novelty of the focal species (i.e. the least experience in resident species) can be expected if no resident species are present in the focal species' guild before the invasion event. The novelty of the focal species gradually decreases with an increasing number of resident species that are in the same guild as the focal species. Subtracting the fraction from 1, we obtain the eco-evolutionary experience of the resident species community ($xp_{Residents}$), with values ranging again between 0 (no applicable experience of resident species with the focal species) to 1 (maximum applicable experience).

Having thus calculated both the eco-evolutionary experience of the focal species (xp_{Focal}) and the experience of the resident species community $(xp_{Residents})$ for different types of interaction, we can return to the framework in Fig. 1 and estimate the probability of the invasion to succeed.

Discussion

In the previous chapters, we introduced a framework that – by adopting an eco-evolutionary perspective – integrates so far unrelated approaches for explaining biological invasions, and we drafted a routine to quantify eco-evolutionary experience, which is the key variable in this framework. It has to be emphasized again that the framework is of conceptual nature. For instance, the assumed relationship between eco-evolutionary experience and invasion success has to be substantiated with empirical data beyond the hypothetical graphs presented in Fig. 1. Furthermore, the quantification routine makes several simplifying assumptions that have to be kept in mind for an appropriate interpretation:

- Species are adapted to virtually all of their biotic interactions in the source area, which constitutes the inherited eco-evolutionary experience that may matter in ecologically similar communities in the target area. In reality, species are not necessarily adapted to all interactions, e.g. due to weak selection pressure, evolutionary trade-offs, or gene flow. Furthermore, we assume there is no significant intraspecific variation in species traits, e.g. among different populations of the same species.
- Adaptation has no costs. Consider, for example, two focal species that face a single predator species of guild R3 from the example in Appendix II in their respective target areas. For both of them, we would calculate $xp_{Focal}=1$ if during their evolution in the source area they adapted to at least one predator species of the guild R3. The same xp value would be computed even if one of the focal species had adapted to additional predator species. In reality, such 'over-adaptation' would probably have generated costs, which could imply disadvantages when compared to the other focal species, but in our model it does not translate into a lower probability of invasion success.

- All interactions are assumed to be equal in strength and frequency. For instance, no distinction is made between generalists and specialists, or whether the focal species interacts in the target area with exactly the same species as in the source area or just with a member of the same guild.
- There is no amplifying effect within interaction types: an interaction partner is counted only once in each type of interaction, even if it maintains more than one 'connection' with the focal species within that interaction type (e.g. when competing with the focal species for several prey species).
- As mentioned above, only a subset of all interactions in the studied food webs is included in the analysis, i.e. direct and single-step indirect interactions, and the number of interacting partners in each guild depends on the particular guild definition chosen.

On a side note, we focused in this paper on novel *biotic* interactions that may influence invasion success in order to demonstrate the usefulness of an eco-evolutionary perspective in invasion research. This is not to argue, of course, against the substantial effect that other factors may have on invasion success as well. The significant influence of abiotic conditions has been indicated, for instance, by studies on the effect of climate change (Hellmann et al. 2008, Walther et al. 2009, Engel et al. 2011). Also, Mitchell et al. (2006, p. 734) correctly pointed out that biotic interactions may be influenced "not only directly through the gain and loss of enemies, mutualists and competitors, but also indirectly by putting interactions with the same species in a different environmental context". Furthermore, among many other factors, the roles of propagule pressure or of intrinsic factors such as (lack of) genetic variability and reproductive systems have to be considered in this context.

We believe that the indices proposed here $(xp_{Focal} \text{ and } xp_{Residents})$ constitute an important first step towards an efficient quantitative estimate of the influence of species' evolutionary legacy on the success of biological invasions. A particular strength of this approach lies in its high flexibility: it allows considering not only food webs but also other ecological networks; different kinds of ecological groupings (ecological guilds, functional groups etc.) can be used; and it is applicable to all living organisms across taxonomic boundaries (e.g. plants and animals alike).

From an applied perspective, the further development of the framework and quantification routine to include less simplifying assumptions is certainly highly desirable and a stimulating research perspective. An important next step is to actually test the usefulness of our framework and the quantification routine for empirical case studies. Also, it should be investigated how the various *xp* values computed for the different types of interaction can best be integrated to provide an *overall* estimate of invasion probability. This could, for instance, be done by reducing complexity (and potential inconsistencies) considering only the most important type(s) of interaction in the respective case study, or it could comprise the development of a single, combined *xp* value.

Conclusion

An integrative and comprehensive conceptual treatment of conclusions derived from findings in both ecological and evolutionary research is still hard to find in invasion ecology. However, as we have outlined above, such an eco-evolutionary perspective would not merely add parenthetical historical information but would increase our potential to uncover invasion patterns. Our framework provides the means for interrelating seemingly isolated ecological invasion hypotheses by identifying implicit eco-evolutionary assumptions (Fig. 1, Appendix I). The framework thus helps to synthesize the conclusions drawn from these hypotheses, providing a stronger basis for a more general understanding of invasion mechanisms and reasons for variation in invasion success. It ties in with the idea of a 'hierarchy of hypotheses' (Jeschke et al. 2012, Heger et al., in press), where overarching conceptual ideas in invasion ecology (e.g. the concept of eco-evolutionary experience) branch into more precise and testable hypotheses at lower levels (e.g. enemy release, EICA, novel weapons etc.). Such a hierarchy helps to systematically organize the specific predictions of the large number of individual hypotheses and the evidence accumulated for or against them (Jeschke et al. 2012). This in turn allows evaluating the more general predictions represented by the complete branch of an overarching idea and to identify more fundamental patterns in biological invasions.

The framework generates new, although still very general conceptions on how invasion success depends on eco-evolutionary experience and emphasizes the importance of considering both interacting sides simultaneously: native and non-native species. It also takes into account that non-native species may take up different ecological roles in the exotic range and allows differentiated conclusions for the major types of ecological interactions that may be affected by the invasion.

We believe that the conceptual insights that can be derived from our framework and the quantification routine can be of significant help to guide future research. Ultimately, this research may lead to effective management measures to prevent the introduction of species that seem particularly 'risky' for a specific target area, or to adopt appropriate mitigation or restoration measures.

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References

- Agrawal AA, Kotanen PM (2003) Herbivores and the success of exotic plants: a phylogenetically controlled experiment. Ecology Letters 6: 712–715. doi: 10.1046/j.1461-0248.2003.00498.x
- Alpert P (2006) The advantages and disadvantages of being introduced. Biological Invasions 8: 1523–1534. doi: 10.1007/s10530-005-5844-z
- Blackburn TM, Cassey P, Duncan RP, Evans KL, Gaston KJ (2004) Avian extinction and mammalian introductions on oceanic islands. Science 305: 1955–1958. doi: 10.1126/science.1101617
- Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. Trends in Ecology & Evolution 26: 333–339. doi: 10.1016/j.tree.2011.03.023
- Blaum N, Mosner E, Schwager M, Jeltsch F (2011) How functional is functional? Ecological groupings in terrestrial animal ecology: toward an animal functional type approach. Biodiversity Conservation 20: 2333-2345. doi: 10.1007/s10531-011-9995-1
- Blondel J (2003) Guilds or functional groups: does it matter? Oikos 100: 223–331. doi: 10.1034/j.1600-0706.2003.12152.x
- Blossey B, Nötzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. Journal of Ecology 83: 887–889. doi: 10.2307/2261425
- Callaway RM, Aschehoug ET (2000) Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. Science 290: 521–523. doi: 10.1126/science.290.5491.521
- Carlsson NOL, Sarnelle O, Strayer DL (2009) Native predators and exotic prey an acquired taste? Frontiers in Ecology and the Environment 7(10): 525–532. doi: 10.1890/080093
- Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Diversity and Distributions 15: 22–40. doi: 10.1111/j.1472-4642.2008.00521.x
- Cavender-Bares J, Ackerly DD, Baum DA, Bazzaz FA (2004) Phylogenetic overdispersion in Floridian oak communities. The American Naturalist 163: 823–843. doi: 10.1086/386375
- Cox GW (2004) Alien species and evolution: the evolutionary ecology of exotic plants, animals, microbes, and interacting native species. Island Press, Washington, DC, 400pp.
- Cox JG, Lima SL (2006) Naiveté and an aquatic-terrestrial dichotomy in the effects of introduced predators. Trends in Ecology & Evolution 21: 674–680. doi: 10.1016/j.tree.2006.07.011
- Daehler CC (2001) Darwin's naturalization hypothesis revisited. The American Naturalist 158: 324–330. doi: 10.1086/321316
- Davis MA (2009) Invasion biology. Oxford University Press, Oxford, 288pp.
- Diez JM, Sullivan JJ, Hulme PE, Edwards G, Duncan RP (2008) Darwin's naturalization conundrum: dissecting taxonomic patterns of species invasions. Ecology Letters 11: 674–681. doi: 10.1111/j.1461-0248.2008.01178.x
- Engel K, Jeschke JM, Tollrian R (2011) Integrating biological invasions, climate change, and phenotypic plasticity. Communicative & Integrative Biology 4: 247–250. doi: 10.4161/ cib.4.3.14885

- Facon B, Genton BJ, Shykoff J, Jarne P, Estoup A, David P (2006) A general eco-evolutionary framework for understanding bioinvasions. Trends in Ecology & Evolution 21: 130–135. doi: 10.1016/j.tree.2005.10.012
- Futuyma DJ (2005) Evolution. Sinauer Associates, Sunderland, 603pp.
- Gurevitch J, Fox GA, Wardle GM, Inderjit, Taub D (2011) Emergent insights from the synthesis of conceptual frameworks for biological invasions. Ecology Letters 14: 407–418. doi: 10.1111/j.1461-0248.2011.01594.x
- Hänfling B, Kollmann J (2002) An evolutionary perspective of biological invasions. Trends in Ecology & Evolution 17: 545–546. doi: 10.1016/S0169-5347(02)02644-7
- Hawkins CP, MacMahon JA (1989) Guilds: the multiple meanings of a concept. Annual Review of Entomology 34(1): 423–451. doi: 10.1146/annurev.en.34.010189.002231
- Heger T, Trepl L (2003) Predicting biological invasions. Biological Invasions 5: 313–321. doi: 10.1023/B:BINV.0000005568.44154.12
- Heger T, Saul W-C, Trepl L (2013) What biological invasions 'are' is a matter of perspective. Journal for Nature Conservation 21: 93–96. doi: 10.1016/j.jnc.2012.11.002
- Heger T, Pahl AT, Botta-Dukat Z, Gherardi F, Hoppe C, Hoste I, Jax K, Lindström L, Boets P, Haider S, Kollmann J, Wittmann MJ, Jeschke JM (in press) Conceptual frameworks and methods for advancing invasion ecology. AMBIO. doi: 10.1007/s13280-012-0379-x
- Hellmann JJ, Byers JE, Bierwagen BG, Dukes JS (2008) Five potential consequences of climate change for invasive species. Conservation Biology 22: 534–543. doi: 10.1111/j.1523-1739.2008.00951.x
- Hokkanen H, Pimentel D (1989) New associations in biological control: theory and practice. Canadian Entomologist 121: 829–840. doi: 10.4039/Ent121829-10
- Hufbauer RA, Torchin ME (2007) Integrating ecological and evolutionary theory of biological invasions. In: Nentwig W (Ed.) Biological invasions. Springer, Berlin, 79–96. doi: 10.1007/978-3-540-36920-2_6
- Inderjit, Cadotte MW, Colautti RI (2005) The ecology of biological invasions: past, present and future. In: Inderjit (Ed) Invasive plants: ecological and agricultural aspects. Birkhäuser Verlag, Basel, 19–43.
- Jeschke JM, Strayer DL (2006) Determinants of vertebrate invasion success in Europe and North America. Global Change Biology 12: 1608–1619. doi: 10.1111/j.1365-2486.2006.01213.x
- Jeschke JM, Gómez Aparicio L, Haider S, Heger T, Lortie CJ, Pyšek P, Strayer DL (2012) Support for major hypotheses in invasion biology is uneven and declining. NeoBiota 14(1): 1–20. doi: 10.3897/neobiota.14.3435
- Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends in Ecology & Evolution 17: 164–170. doi: 10.1016/S0169-5347(02)02499-0
- Kondoh M (2006) Contact experience, alien-native interactions, and their community consequences: a theoretical consideration on the role of adaptation in biological invasions. In: Cadotte MW, McMahon SM, Fukami T (Eds) Conceptual ecology and invasion biology. Springer, Dordrecht, 225–242.

- Lee CE (2002) Evolutionary genetics of invasive species. Trends in Ecology & Evolution 17: 386–391. doi: 10.1016/S0169-5347(02)02554-5
- Losos JB (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. Ecology Letters 11: 995–1003. doi: 10.1111/j.1461-0248.2008.01229.x
- Mitchell CE, Agrawal AA, Bever JD, Gilbert GS, Hufbauer RA, Klironomos JN, Maron JL, Morris WF, Parker IM, Power AG, Seabloom EW, Torchin ME, Vazquez DP (2006) Biotic interactions and plant invasions. Ecology Letters 9: 726–740. doi: 10.1111/j.1461-0248.2006.00908.x
- Nussey DH, Postma E, Gienapp P, Visser ME (2005) Selection on heritable phenotypic plasticity in a wild bird population. Science 310: 304–306. doi: 10.1126/science.1117004
- O'Dowd DJ, Green PT, Lake PS (2003) Invasional 'meltdown' on an oceanic island. Ecology Letters 6: 812–817. doi: 10.1046/j.1461-0248.2003.00512.x
- Orians CM, Ward D (2010) Evolution of plant defenses in nonindigenous environments. Annual Review of Entomology 55: 439–459. doi: 10.1146/annurev-ento-112408-085333
- Pianka ER (2000) Evolutionary ecology. Benjamin Cummings, Addison-Wesley-Longman, San Francisco, 528pp.
- Procheş Ş, Wilson JRU, Richardson DM, Rejmánek M (2008) Searching for phylogenetic pattern in biological invasions. Global Ecology and Biogeography 17: 5–10. doi: 10.1111/j.1466-8238.2007.00333.x
- Ricciardi A, Atkinson SK (2004) Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. Ecology Letters 7: 781–784. doi: 10.1111/j.1461-0248.2004.00642.x
- Richards CL, Bossdorf O, Muth NZ, Gurevitch J, Pigliucci M (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. Ecology Letters 9: 981–993. doi: 10.1111/j.1461-0248.2006.00950.x
- Richardson DM (Ed) (2011) Fifty years of invasion ecology: the legacy of Charles Elton. Wiley-Blackwell, Oxford, 456pp.
- Richardson DM, Allsopp N, D'Antonio CM, Milton SJ, Rejmánek M (2000) Plant invasions the role of mutualisms. Biological Reviews 75: 65–93. doi: 10.1017/S0006323199005435
- Root RB (1967) Niche exploitation pattern of blue-gray gnatcatcher. Ecological Monographs 37: 317–350. doi: 10.2307/1942327
- Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG (2001) The population biology of invasive species. Annual Review of Ecology and Systematics 32: 305–332. doi: 10.1146/annurev.ecolsys.32.081501.114037
- Sax DF, Brown JH (2000) The paradox of invasion. Global Ecology and Biogeography 9: 363–371. doi: 10.1046/j.1365-2699.2000.00217.x
- Sax DF, Stachowicz JJ, Brown JH, Bruno JF, Dawson MN, Gaines SD, Grosberg RK, Hastings A, Holt RD, Mayfield MM, O'Connor MI, Rice WR (2007) Ecological and evolutionary insights from species invasions. Trends in Ecology & Evolution 22: 465–471. doi: 10.1016/j.tree.2007.06.009
- Sax DF, Stachowicz JJ, Gaines S (Eds) (2005) Species invasions: insights into ecology, evolution, and biogeography. Sinauer Associates, Sunderland, 495pp.

- Sih A, Bolnick DI, Luttbeg B, Orrock JL, Peacor SD, Pintor LM, Preisser E, Rehage JS, Vonesh JR (2010) Predator–prey naïveté, antipredator behavior, and the ecology of predator invasions. Oikos 119: 610–621. doi: 10.1111/j.1600-0706.2009.18039.x
- Sol D, Bacher S, Reader SM, Lefebvre L (2008) Brain size predicts the success of mammal species introduced into novel environments. The American Naturalist 172: S63–S71. doi: 10.1086/588304
- Strauss SY, Webb CO, Salamin N (2006) Exotic taxa less related to native species are more invasive. Proceedings of the National Academy of Sciences USA 103: 5841–5845. doi: 10.1073/pnas.0508073103
- Strayer DL, Eviner VT, Jeschke JM, Pace ML (2006) Understanding the long-term effects of species invasions. Trends in Ecology & Evolution 21: 645-651. doi: 10.1016/j. tree.2006.07.007
- Styrsky JD, Eubanks MD (2007) Ecological consequences of interactions between ants and honeydew-producing insects. Proceedings of the Royal Society of London Series B: Biological Sciences 274: 151–164. doi: 10.1098/rspb.2006.3701
- Thuiller W, Gallien L, Boulangeat I, de Bello F, Münkemüller T, Roquet C, Lavergne S (2010) Resolving Darwin's naturalization conundrum: a quest for evidence. Diversity and Distributions 16: 461–475. doi: 10.1111/j.1472-4642.2010.00645.x
- Walther G-R, Roques A, Hulme PE, Sykes MT, Pyšek P, Kühn I, Zobel M, Bacher S, Botta-Dukát Z, Bugmann H, Czúcz B, Dauber J, Hickler T, Jarošík V, Kenis M, Klotz S, Minchin D, Moora M, Nentwig W, Ott J, Panov VE, Reineking B, Robinet C, Semenchenko V, Solarz W, Thuiller W, Vilà M, Vohland K, Settele J (2009) Alien species in a warmer world: risks and opportunities. Trends in Ecology & Evolution 24: 686–693. doi: 10.1016/j.tree.2009.06.008
- Wilson JB (1999) Guilds, functional types and ecological groups. Oikos 86: 507–522. doi: 10.2307/3546655

Appendix I

The shared eco-evolutionary basis of major hypotheses in invasion ecology

The concept of 'eco-evolutionary experience' posits that biotic interactions maintained during the evolutionary history of species influence the outcome of interactions between native and introduced species in present times, i.e. (a) the invasion success of the introduced species and (b) the responses of natives. Several major hypotheses for explaining invasion success can be directly related to this concept based on their implicit reference to the logical consequence of a species being introduced into an area where it has not evolved (for references see main text):

- *a)* Specialized, i.e. eco-evolutionarily highly experienced native enemies of the introduced species may be missing ('enemy release hypothesis').
- *b)* Reduced predation due to inexperienced native predators (herbivores) may allow the introduced species to allocate more resources to traits that increase its competitive abilities ('evolution of increased competitive ability hypothesis').
- *c)* The introduced species may be inexperienced with native enemies and may therefore lack appropriate defence mechanisms ('new associations hypothesis').
- *d)* Introduced species with close relatives in the target area may be less successful because native predators may already be experienced with native congeneric prey species ('Darwin's naturalization hypothesis').
- *e)* Native prey species may be unprepared, i.e. inexperienced for effectively countering novel predatory behaviour of an introduced species ('naïve prey hypothesis').
- *f)* Native species may not be adapted to, i.e. may be inexperienced with specialized competitive strategies of the introduced species ('novel weapons hypothesis').
- *g)* Mutualistic interactions may fail to develop because of missing experience between native and non-native species ('missed mutualisms hypothesis').
- *h)* Mutualistic interactions between a native and non-native species may be possible, provided that the degree of experience is high enough in both interaction partners ('mutualist facilitation hypothesis').
- *i)* Species that have evolved a strong commensal affiliation to humans may benefit from this eco-evolutionary experience when introduced to areas dominated by humans. This may be especially true for Eurasian species: they coevolved with Europeans and their plants, pathogens and livestock, which were dispersed all over the world during the European Imperialism period ('human commensals and imperialism hypothesis').
Appendix II

Routine for the quantification of eco-evolutionary experience: a food webbased example

- 1. Identify direct interactions and single-step indirect interactions (i.e. including one intermediate species) of the focal species in the food web of its source area and in the food web of the (potential) target area (see example in Fig. A).
- 2. Define ecological guilds (or other appropriate ecological groupings) for each type of ecological interaction (focal species acting as prey, predator, competitor or indirect mutualist). Assign the focal species and its interaction partners in the source and target area to the ecological guilds.



Figure A. Hypothetical food webs in freshwater lakes in source and target area. Circles represent species (F = focal species), different shading and patterning indicate different guilds (see steps 2 and 3).

Quantification of the focal species' eco-evolutionary experience (xp_{Focal}) :

- 3. Determine the number of species that interact with the focal species per ecological guild in the source and target area, separately for each type of interaction (Table A).
- 4. Calculate the xp_{Focal} index (Eq. 2) for each type of interaction, obtaining the eco-evolutionary experience of the focal species regarding its interaction with resident species in the food web of the target area.

Quantification of the resident species' eco-evolutionary experience $(xp_{Residents})$:

- 5. Determine the number of resident species in the target area that are members of the same ecological guild as the focal species (regardless if they interact with the focal species or not), separately for each type of interaction (Table B).
- 6. Calculate the $xp_{Residents}$ index (Eq. 3) for each type of interaction, obtaining the eco-evolutionary experience of the resident species community regarding its interaction with the introduced focal species.

Table A. Numbers of species per guild that interact with the focal species in the food webs of the source and target area (taken from Fig. A), and the respective eco-evolutionary experience of the focal species (xp_{Focal}) in the target area (R1-R5: predator guilds, P1-P5: prey guilds, C1-C5: competitor guilds, M1-M5: mutualist guilds).

Type of interaction Interaction partners of the focal species	No. of species in guild <i>i</i> in source area S					No. of species in guild <i>i</i> in target area <i>T</i>					<i>xp</i> _{Focal}
<i>i</i> =	<i>R1</i>	R2	R3	R4	R5	R1	R2	R3	R4	R5	
Predators	2	-	-	-	-	1	-	-	-	-	1.00
<i>i</i> =	P1	P2	P3	P4	P5	P1	P2	P3	P4	P5	
Prey	2	1	-	-	-	-	-	1	1	2	0.43
<i>i</i> =	C1	C2	СЗ	C4	C5	C1	C2	СЗ	C4	C5	
Competitors	-	-	-	-	-	1	1	1	-	-	0.00
<i>i</i> =	M1	M2	М3	M4	M5	M1	M2	М3	M4	M5	
Indirect mutualists	4	1	-	-	-	3	4	-	-	-	0.75

Table B. Number of resident species in the target area that are members of the same guild as the focal species (note that species numbers are exemplary and not directly deducible from Fig. A), and the respective eco-evolutionary experience of the native community ($xp_{Reidens}$) with the focal species.

	No. of resident species in same guild as the focal species	xp _{Residents}
Predators	1	0.50
Prey	0	0.00
Competitors	3	0.75
Indirect mutualists	2	0.67