Biol Invasions (2012) 14:547–556
DOI 10.1007/s10530-011-0094-8

ORIGINAL PAPER

Latitudinal shifts of introduced species: possible causes and implications

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Received: 26 January 2011 / Accepted: 22 August 2011 / Published online: 4 September 2011

Abstract This study aims to document shifts in the latitudinal distributions of non-native species relative to their own native distributions and to discuss possible causes and implications of these shifts. We used published and newly compiled data on intercontinentally introduced birds, mammals and plants. We found strong correlations between the latitudinal distributions occupied by species in their native and exotic ranges. However, relatively more non-native species occur at latitudes higher than those in their native ranges, and fewer occur at latitudes lower than those in their native ranges. Only a small fraction of species examined (i.e. <20% of animals and <10% of plants) have expanded their distributions in their exotic range beyond both high- and low-limits of their native latitudes. Birds, mammals and plants tended to shift their exotic ranges in similar ways. In addition, most non-native species (65–85% in different groups) have not reached the distributional extent observed in their native ranges. The possible drivers of latitudinal shifts in the exotic range may include climate change, greater biotic resistance at lower latitudes, historical limitations on ranges in native regions, and the impacts of humans on species distributions. The relatively restricted distribution of most species in their exotic range highlights the great potential of future spread of most introduced species and calls for closely monitoring their directional spread under climate change.

Keywords Climate change · Invasion potential · Land use · Niche · Risk assessment · Species range

Introduction

Non-native populations have a profound influence on native species and ecosystems across the globe, causing extinctions and changes in ecosystem functioning (Mooney and Hobbs 2000). These impacts

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Electronic supplementary material The online version of this article (doi:10.1007/s10530-011-0094-8) contains supplementary material, which is available to authorized users.

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have led to interest and extensive study of the distribution of non-native populations—hereafter referred to as non-native species (e.g., Lonsdale 1999; Sax et al. 2002, 2005; Leprieur et al. 2008; Pyšek et al. 2010). A persistent theme in these studies has been a search for characteristics of non-native species that predict their capacity to spread broadly in an introduced region (e.g., Baker and Stebbins 1965; Lockwood et al. 2007; Davis 2009). Much work has indicated that species traits can be used to predict their potential to spread and the eventual size of their non-native distribution (e.g., Richardson et al. 1994; Rejmánek and Richardson 1996; Smith et al. 2007). Recent work, however, has indicated that in addition to species traits, human influences on the environment and the size of human economies can be strongly correlated with the distributional patterns of large numbers of non-native species (Leprieur et al. 2008; Pyšek et al. 2010).

The distribution of non-native species is also presumed to be strongly influenced by climate. For instance, the concept of 'climate matching' suggests that species have the potential to become naturalized only in places with climates similar to those experienced in their own native ranges (e.g. Mack 1996; Thuiller et al. 2005). Although there is support for the importance of climate matching in limiting the distribution of non-native species, much of this support suggests that a species' native climatic distribution is not a perfect predictor of its potential non-native distribution. For example, most studies that have compared the climate-niche envelope of species' native and naturalized distributions have found that non-native species are distributed at least in some places that they are not predicted based solely on their native climatic distributions (Beerling et al. 1995; Welk et al. 2002; Broennimann et al. 2007; Fitzpatrick et al. 2007; Alexander and Edwards 2010; Gallagher et al. 2010). In some cases, climate appears to be a particularly poor predictor of potential distributions of non-native species, e.g., species with small native distributions (and presumably restricted native climatic distributions) that have nonetheless acquired extensive non-native distributions, such as the Monterey pine, *Pinus radiata* (Sax et al. 2007). Additional work, particularly in the context of global climate change, is continuing to pursue the relative influence of climate on non-native species distributions (e.g., Thuiller et al. 2005; Peterson et al. 2008; Walther et al. 2009; Britton et al. 2010). But given the consistent limitations of climate as an ideal predictor of non-native species distributions, it is important to consider the utility of other potentially informative indicators.

Latitudinal patterns and the search for latitudinal 'rules of thumb' for non-native species distributions have the potential to be useful, but this topic has not been addressed comprehensively. This is unfortunate since latitude integrates many aspects of biotic, abiotic and human influences that are believed to be important in limiting species distributions—such as climate, soil type, biotic diversity, and land use. Consequently, examining non-native distributions in the context of latitude, which can be easily quantified, can potentially inform the limitations and potential expansion of distributions of non-native species, particularly at a large scale. Indeed, work conducted to-date has shown latitude to be an important predictor of non-native species distributions and mediator of ecological processes affecting distributions. Colautti et al. (2009) found that differences in species performance between native and naturalized ranges were strongly influenced by the latitude at which species performance was measured. Rejmánek (1996) and Lonsdale (1999), among others, have observed that temperate mainlands are more invaded than tropical ones. Sax (2001) showed that non-native species of many taxonomic groups on many continents show predictable latitudinal gradients in species richness and geographic range size. Sax (2001) also showed that birds and mammals were less likely to become naturalized at latitudes lower than those in their native range than at latitudes higher than those in their native range. Pyšek and Richardson (2006) found a general pattern of decreasing naturalization rates with increasing latitude in plants. Finally, over paleontological timescales, Jablonski (2008) has shown that temperate latitudes are generally invaded from species that inhabit tropical latitudes. Thus, we believe that a large-scale study is needed to identify the existence and predictive importance of latitude in limiting non-native species distributions.

Here we examine whether there are rules of thumb regarding how naturalized species' latitudinal distributions compare to their own native distributions. Specifically, we compare the highest and lowest latitudinal-limits between the introduced and their native ranges, with a particular focus on whether non-native species approach or exceed the latitudinal limits experienced in their own native distributions. Species included in this study are birds and mammals introduced to continents and islands across the world and plants introduced between eastern Asia and North America. Our primary goal is to address whether and to what extent non-native species might have superseded their native latitudinal distributions. We discuss the possible mechanisms, consequences, and implications of such observations, while bearing in mind the differences in observed patterns among taxonomic groups, particularly between woody and herbaceous plants or between birds and mammals.

Methods

We analyzed latitudinal data for a total of 825 species from different continents across the globe, including 147 bird species, 85 mammal species, and 593 plant species (512 introduced into North America from eastern Asia; 81 introduced into eastern Asia from North America). The data for birds and mammals were collected from various published sources, as described by Sax (2001). Range-limits for each species were recorded in both the native and naturalized ranges on continents and islands worldwide (see Sax 2001 for details). We recorded absolute latitudinal limits, irrespective of the hemisphere in which a species occurred, such that the range boundary closest to the equator was 'lowest' and the one closest to a pole was 'highest'. A species' lowest and highest latitudinal limits in introduced regions were recorded from different continents and islands if introduced to multiple locations, such that only a single global highest and a single global lowest latitudinal limit were used for each naturalized species considered in our analyses. Only the introduced bird and mammal species that have maintained stable or growing populations for multiple generations without human assistance (i.e. naturalized species) were included in the analyses.

For plants, we used established exotic species exchanged between eastern Asia and North America (for detailed information about the database, see Guo et al. 2006). Eastern Asia and North America are similar in terms of geographic area and climatic gradients. Both regions are located in the northern hemisphere and have tropical, subtropical, temperate, and boreal areas along a latitudinal gradient. This close matching provides unique opportunities for comparing species range size and location in terms of latitude and climate zone in native and naturalized regions. Because many species are distributed in more than one climatic zone, the continuous and more-or-less parallel arrangements of multiple climatic zones in eastern Asia and North America provide a full spectrum of latitude and climate gradients from the tropics to the arctic, within which the spread of a species in its recipient region can be meaningfully compared to that in its native region (see examples of these climatic gradients in Fig. S1). Eastern Asia and North America each have received many non-native species from each other and elsewhere and the numbers continue to increase due to growing trade and human travel between the two regions (Guo et al. 2006). We analyzed herbaceous and woody species separately as well as all species combined. The species with southern limits reaching the southernmost coastal provinces and states were excluded because such distributions might not represent the furthest South that those species could tolerate if more land were available, particularly as the two regions have different levels of connection with tropical regions.

We examined the latitudinal extent, latitudinal midpoint, the lowest and highest latitudinal limits of each species in both its naturalized and its native geographic distribution, as recorded to the nearest 1° of latitude. Latitudinal extent was calculated, for both the native and naturalized ranges, as the difference between the highest and lowest latitudinal limits of a species' distribution. For species present in both the northern and southern hemisphere, the highest latitude was recorded as the point furthest from the equator, whereas the lowest latitude was recorded as the point closest to the equator. Latitudinal midpoint values were calculated as the point equidistant between a species' highest and lowest latitudinal points of distribution. If a species' distribution spanned the equator then its lowest latitude was recorded as zero and its latitudinal midpoint value was calculated relative to the single hemisphere where it has the largest latitudinal extent, such that the value equals the average of its lowest latitude of occurrence (i.e., 0) and its highest latitude of occurrence.

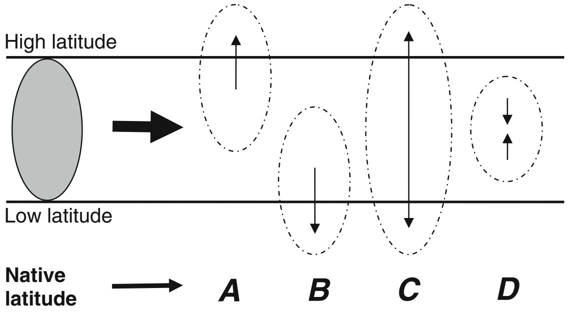

Fig. 1 Four possible scenarios of latitudinal shifts of exotic species based on the direction and extent of their naturalized distribution relative to their own native distribution. *A* net poleward, *B* net equatorward, *C* bidirectional shifts (i.e. both high and low latitudes expanded), and *D* no shift (i.e. both high and low latitudes constrained)

We examined trends in differences between species' native and naturalized latitudinal distributions in several ways. First, we used least square regression to examine the correspondence in species lowest, midpoint and highest latitudes within their native and naturalized distributions. We compared the regression slopes as they indicate whether and to what extent the species from different latitudinal zones may be found in higher (or lower) latitudes after introduction. Second, we examined the percentage of species in each taxonomic category whose naturalized ranges, relative to their native ranges, showed a shift in a net poleward, net equatorward, or bidirectional manner, as well as those that showed no shift (Fig. 1). Third, we compared differences in the average latitudinal extent of natives versus exotics for each of our taxonomic groups with paired *t* tests. Fourth, for a set of 60 introduced plant species with known dates of introduction we examined the relationship between time since first known occurrence and total latitudinal extent in their naturalized range using regression analysis.

Results

Comparisons of individual species latitudinal distributions showed qualitatively similar patterns among taxonomic groups. We observed a strong, positive correlation between the latitudinal midpoints of species' native and naturalized distributions for all taxa examined: mammals, birds and plants (Fig. 2; Table 1). The slopes and intercepts of these relationships varied among taxonomic groups, but most showed a slope <1 (Fig. 2; Table S1). The strongest correlations were found for plants, followed by mammals and then birds (Table 1). The lowest and highest latitudes occupied were significantly correlated for all comparisons between native and naturalized ranges. However, after making a Bonferroni correction for multiple comparisons, one relationship, the lowest latitude comparison of North American native plants introduced to eastern Asia, was no longer significant; Table 1). The latitudinal midpoint of distributions in naturalized regions tended to be higher on average than in native regions. This was true in aggregate, i.e. the average latitudinal midpoint value of the naturalized range exceeded that of the native range by 0.23, 3.83, 2.47 and 0.09°, respectively, for birds, mammals, plants introduced to North America and plants introduced to eastern Asia. It was also true when considering the distributions of individual species, where more points were above the lines of equality than below them for mammals (67%) and plants from Asia introduced to North America (79%), but was not true for birds (50%) or plants from North America introduced to Asia (40%; Fig. 2).

The latitudinal distribution of individual species in their naturalized ranges varied widely from those observed in their native ranges (Table 2). The majority of species of each taxonomic group examined (birds, mammals and plants) extended their non-native latitudinal distribution beyond one or both of their native latitudinal limits (i.e. sum of categories A, B and C; Table 2); a minority of non-native species were entirely positioned within their native latitudinal limits within their naturalized ranges (category D; Table 2). Net poleward shifts were more common than net equatorward shifts for birds, mammals and plants from eastern Asia introduced to North America, whereas net equatorward shifts were more common for plants from North America introduced to eastern Asia (Table 2). Bidirectional shifts, i.e. shifts beyond the native high- and low-latitude boundary, within the naturalized range occurred, but rarely—16, 20, 9 and 8% respectively of birds, mammals, plants from eastern Asia and plants from North America showing this response (Table 2). Although there were many species that exceeded native latitudinal distributions, few species

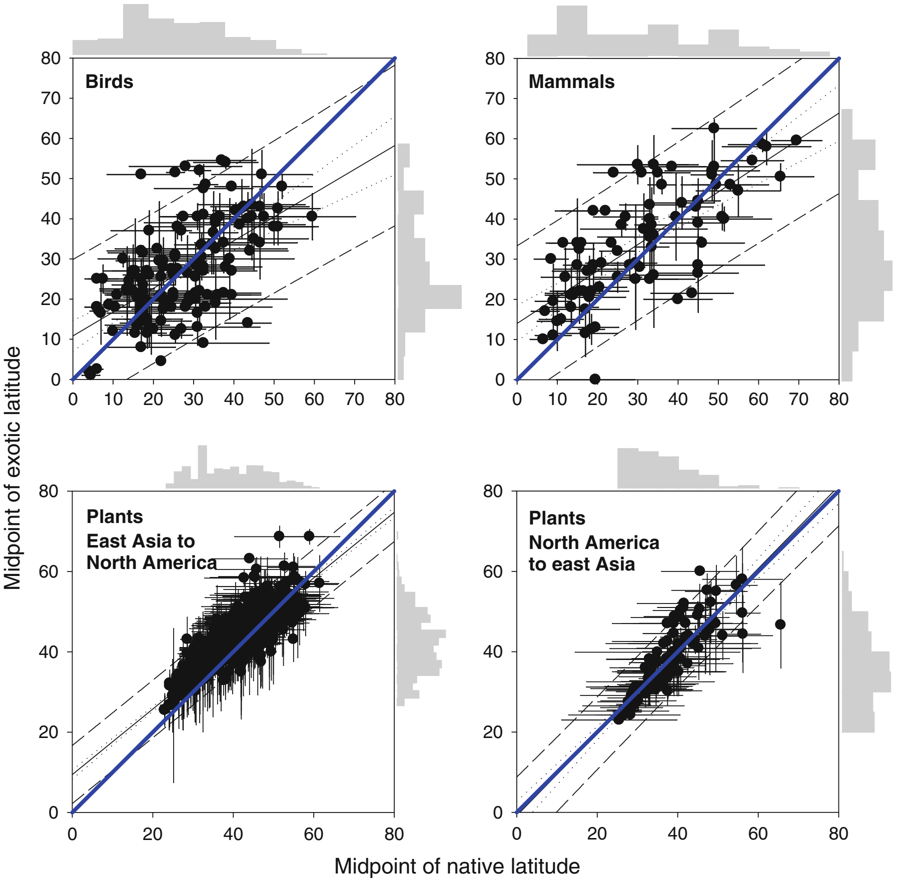

Fig. 2 The correlation between the latitudinal midpoint of species' native and naturalized distributions for birds and mammals (introduced worldwide), for plants from eastern Asia introduced into North America, and for plants from North America introduced into eastern Asia; see the text for a description of how the midpoints were calculated. The horizontal and vertical lines of each dot are the latitudinal extents of species in the native and naturalized regions, respectively [rescaled as (*highest-mean*)/*2*]. The *dotted* and *dashed lines* are 95% confidence and prediction intervals, respectively. The *shaded bars* represent frequency of species in latitudinal zones. The *solid diagonal lines* are *lines* of equality between the *x* and *y*-axis

Table 1 Correlation coefficients (r^2) between species latitudinal extent, mid-latitude, and low- and high-latitude in their native and exotic ranges for birds and mammals (introduced worldwide), for plants from eastern Asia introduced into North America, and for plants from North America introduced into eastern Asia

Latitude	Birds ($n = 147$)	Mammals ($n = 85$)	Plants native to eastern Asia and exotic to North America ($n = 512$)	Plants native to North America and exotic to eastern Asia ($n = 81$)
Latitudinal extent	0.08	0.06	**0.24**	0.13
Lowest limit	**0.22 (0.36)**	**0.38 (0.40)**	**0.35**	0.17
Mid-latitude	**0.35**	**0.53**	**0.79**	**0.75**
Highest limit	**0.51 (0.68)**	**0.42 (0.62)**	**0.73**	**0.72**

All values are significant ($P < 0.05$) if calculated for individual comparisons, except for latitudinal extent of birds and mammals, which were marginally significant ($P = 0.07$); however, after performing a Bonferroni correction for multiple tests, only those values in bold-face are significant. Correlation coefficients in parentheses are from Sax (2001) using data from the northern hemisphere only, which showed stronger correlations between high than low-latitude limits. Equations for each of these relationships are available in Table S1

did so by large distances—defined here as exceeding native latitudinal limits by 5 or more degrees of latitude (reported as values in parentheses in Table 2). Among plants, herbaceous species were more likely than woody plant species to have limited distributions in their naturalized range, with the

Table 2 The percentage of exotic species with naturalized distributions shifted relative to native latitudes occupied (as illustrated in Fig. 1) for birds and mammals introduced worldwide, for eastern Asian plants introduced into North America, and for North American plants introduced into eastern Asia

	Birds ($n = 147$)	Mammals ($n = 85$)	Plants: Eastern Asia to North America ($n = 512$)	Plants: North America to eastern Asia ($n = 81$)
A. Net poleward shift	31 (1)	40 (7)	40 (6)	6 (0)
B. Net equatorward shift	15 (1)	10 (1)	12 (11)	52 (1)
C. Bidirectional expansion	16 (5)	20 (6)	9 (8)	8 (7)
D. No shift	38 (93)	30 (86)	39 (75)	34 (92)

Numbers in parentheses signify the percentage of exotic species that have shifted by more than 5° beyond (A) their native high-latitude limit, (B) their native low-latitude limit, (C) both high- and low-latitude limits, or (D) occur within 5° North of their native high-latitude and 5° South of their native low-latitude limits

extreme case being herbaceous plants introduced to North America, for which 50% were constrained entirely within their native latitudinal limits. In general, however, woody and herbaceous species both showed qualitatively similar patterns as plants overall (Table 2, Table S2).

Most introduced species examined had larger latitudinal extents (i.e. range size as measured in the North–South direction) in their native than in their naturalized ranges (86% of birds, 68% of mammals, 70% of eastern Asian herbs, 66% of eastern Asian woody plants, 82% of North American herbs, and 76% of North American woody plants). For birds and mammals, mean latitudinal extents were significantly larger in the native than in the naturalized range (birds: 29.68° vs. 12.41°, mammals: 27.44° vs. 16.88°) (Fig. 3, Table S3). Plants also showed larger mean latitudinal extents in the native than in the naturalized range (Fig. 3; Table S3); herbaceous and woody plants native to eastern Asia had larger native than naturalized latitudinal extents (19.10° vs. 14.15° and 19.00° vs. 14.51°, respectively); similarly herbaceous and woody plants native to North America had larger latitudinal extents in their native than naturalized ranges (22.58° vs. 11.65°, and 12.33° vs. 5.04°, respectively). These differences in species' latitudinal extent led to marginally significant relationships between range size in the native and naturalized range for birds ($r^2 = 0.08$, $P = 0.07$) and mammals ($r^2 = 0.06$, $P = 0.07$), and significant relationships for eastern Asian plants in North America ($r^2 = 0.24$, $P < 0.001$) and North American plants in eastern Asia ($r^2 = 0.13$, $P < 0.001$). Finally, for plants, we were also able to examine patterns of latitudinal extent over time. This examination showed a strong positive relationship between total latitudinal extent occupied in the naturalized range and the amount of time since introduction ($r^2 = 0.27$, $P < 0.001$), a pattern that held for plants introduced into eastern Asia from North America (Guo et al. 2006). However, native latitudinal distribution did not have any effect on this range size–time relationship when relative latitudinal extent was used (i.e., total latitudinal extent occupied in the naturalized range/total latitudinal extent occupied in the native range) to reexamine the latitudinal extent-time relationship ($r^2 = 0.02$, $P > 0.05$).

Discussion

Several patterns emerge from our comparisons between native and naturalized latitudinal distributions for the three groups of species, i.e., birds, mammals, and plants. Despite the strong positive correlations between native and exotic latitudes, in general, all three groups of species exhibit a trend of poleward shifts in latitude after introduction. We discuss these findings and their implications below.

Strong and positive correlations exist between the latitudes occupied in native and naturalized regions for all introduced taxa examined in this study (Fig. 2; Table 1). For all taxa, the correlations were highest for mid-latitude followed by the highest latitude and the lowest latitude. Among the three major taxonomic groups, plants showed the strongest correlations for mid-latitude and highest-latitude distributions,

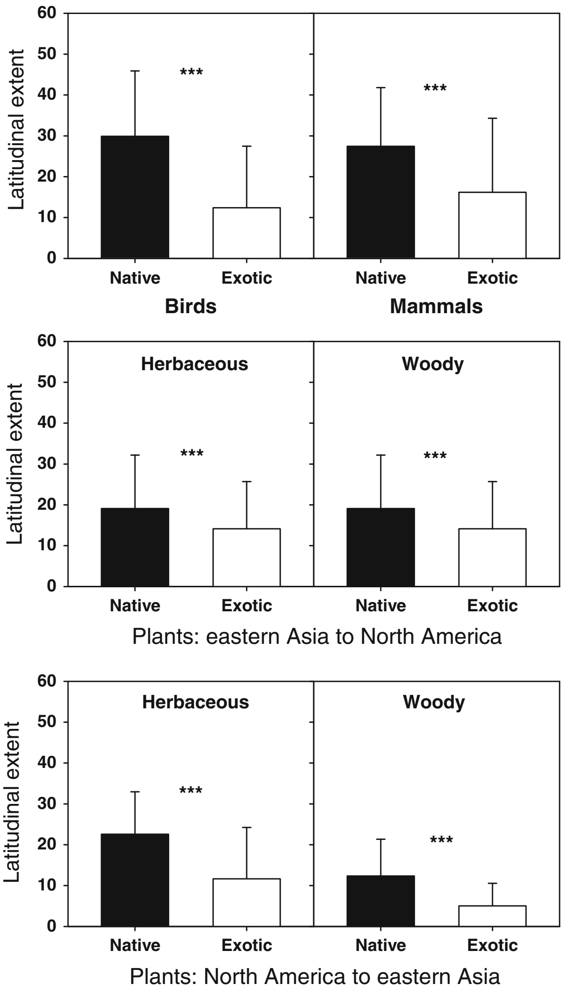

Fig. 3 Mean latitudinal extent (and standard deviation) of species in their native (*solid bars*) versus exotic ranges (*open bars*). Most species have much larger latitudinal extents in their native ranges than in their exotic ranges (Paired *t* tests; *** $P < 0.0001$)

whereas mammals and birds showed stronger correlations for low latitude limits than plants. The latter difference could be explained by our truncation of the list of plants examined to only include those whose distributions did not extend south of the study areas. However, the correlation between native and non-native high-latitude limits of birds and mammals when considering comparisons made solely between continents in the northern hemisphere is similar to the correlation for plants (Table 1). This suggests that the relationship between species native and naturalized high-latitude limits may be conserved across a range of taxonomic groups (e.g., Kaufman 1995; Sax 2001).

The relative strength of all these correlations, on the one hand, is not surprising given that naturalized species might be expected to occupy climate-space that is similar to that in their native ranges, but, on the other hand, is somewhat surprising because many species may have been introduced to latitudes beyond those of their native ranges and because of the anticipated statistical noise in examining taxa whose naturalized ranges are still likely to be expanding. For example, differences in the time of introduction among naturalized species may explain why we did not observe clear differences between herbaceous and woody species with respect to the magnitude of shifts in latitude, as expected due to their differences in dispersal ability and the length of life cycles. However, the strong correlations appear to indicate the strength of conserved tolerances for abiotic conditions and biotic interactions between species native and naturalized ranges. Such conservatism would be consistent with examinations of paleo-disjunct plants; Ricklefs and Latham (1992) and Qian and Ricklefs (2004) found that adaptive responses of most disjunct genera of native plants between eastern Asia and North America to climate conditions have generally been preserved over time between continents.

There is evidence that species naturalized ranges are displaced poleward, on average, relative to their native ranges. This is apparent both in the asymmetries in species tendency to exceed high- versus low-latitude native limits in their naturalized range (Table 2) and as a consequence of the displacement of species latitudinal midpoints in their naturalized versus native distributions (Fig. 2). This pattern of poleward displacement appears to hold for all taxonomic groups examined, i.e., birds, mammals and plants, although not for plants introduced from Asia to North America (Fig. 2, Table 2). A pattern of poleward displacement is intriguing because it is unlikely to be explained as a statistical artifact, as neither a systematic poleward nor equatorward shift in exotic distributions is a necessary outcome of species introductions amongst multiple regions of the world.

Possible mechanisms

The poleward shift in naturalized versus native distributions could be due to several possible reasons.

First, these poleward shifts could be driven by human activities, such as biases in where species are introduced or how species spread in response to human modifications of the environment. For example, the generally lower latitudinal distribution of North American plants in eastern Asia could be due to the fact that human population is concentrated at lower latitudes in eastern Asia than in North America (e.g. Harrison and Pearce 2000). Second, recent changes in climate associated with global climate change could drive this pattern. This might be especially true for the species with strong dispersal ability, which would allow them to rapidly track and fill newly available climate space. This also could occur as an artifact of having better, more current records for species naturalized distributions than for their native distributions. In this case, recent records of species naturalized distributions would include recent advances that occurred in response to climate change, whereas records of natives would only show historic distributions. Alternatively, species might track climate change more closely in their exotic than their native ranges, either because people move them in response to changing conditions or because they are less inhibited (e.g. by the presence of co-evolved predators and competitors) from tracking environmental conditions. Third, poleward shifts could occur if species are differentially able to invade areas poleward of their native distributions (Sax 2001). This is consistent with observations that mainland tropical areas are particularly difficult to invade, possibly because of the higher biotic resistance or relatively lower degree of disturbance than in temperate regions (Sax 2001; Fine 2002). Fourth, this pattern might occur because of factors that make naturalized species less likely to occupy latitudes as near to the equator as they occupy in their own native ranges. The low-latitude occurrences of many species' native ranges were likely colonized during cooler, Pleistocene conditions and are disjunct from other portions of the range; consequently, naturalized species, given their relatively short occupancy in a new region are unlikely to have colonized the low-latitude extremes occupied in their own native ranges. Fifth, species with native distributions at lower latitudes might not be in equilibrium with their potential climatic tolerances, resulting in shifts when introduced to higher latitudes in a new range. This could occur, for example, for species whose native low-latitudinal limits are from islands, which are more numerous at more equatorial latitudes, and which historically were limited by lack of habitat from dispersing to higher latitudes (e.g., Dlugosch and Parker 2008). Finally, poleward shifts could occur because environmental conditions vary among equal latitudes on different continents. While this explanation seems unlikely to provide a general explanation for the birds and mammals we examined, because their introductions and native origins are worldwide, it may explain the discrepancy in patterns between reciprocal plant invasions in North America and eastern Asia. The same latitude in eastern Asia is somewhat colder in winter than in North America, and at any given latitude in the west of eastern Asia the summers are considerably cooler than at the same latitude in North America (Fig. S1). Thus, if species' occupied the same climatic conditions in their native and exotic range we would expect species to move poleward when introduced from Asia to North America and equatorward when introduced from North America to Asia, both of which appear to be true (Fig. 2, Table 2). This suggests an effect of climate niche conservatism. Distinguishing between these hypotheses would improve understanding of what limits species' distributions and help predict the future impacts of introduced species, particularly under climate change.

Consequences and implications

Several 'rules of thumb' regarding latitudinal comparisons of native and naturalized ranges emerge from our analyses, each of which has important implications for predicting naturalized species distributions. First, latitudinal comparisons of native and naturalized distributions show that native latitudinal distribution provides a reasonable first-cut prediction about naturalized latitudinal distributions. This is important because when lacking any other information it allows initial predictions (albeit ones that need to be qualified) to be generated. Second, the latitudinal extents of most naturalized species are currently much narrower than those observed in the native range. This is important because it suggests that most naturalized species still have room to expand within their naturalized distribution. Third, species generally are more likely to exceed native poleward limits than equatorward limits. This is important because it suggests that predictions of invasion risk are likely to be most fallible at high-latitude margins; it also begs for a careful climate niche analysis of poleward range limits, so as to better characterize the role of climate in limiting poleward expansion of naturalized species. Fourth, the patterns observed are fairly robust among birds, mammals and vascular plants. This is interesting because it suggests that latitude is a good proxy variable for multiple taxonomic groups, suggesting the possibility that it may be a useful predictor of naturalized distributions for taxonomic groups not considered in our analyses.

The pattern of poleward displacement of naturalized distributions relative to native ones poses special implications. Although identifying the precise mechanisms for the observed range shifts still requires considerable effort, the fact that poleward shifts have occurred and that these may continue in the future has important ecological consequences at local, regional, and global scales. For example, an important question is whether overall diversity at higher latitudes would increase due to poleward shifts of many species—both native and exotic (Jackson and Sax 2010). Although, as expected, the responses of introduced species to climate change and land use are highly individualistic, the poleward (and upward) shift of many species could have significant implications for invasion biology, management, and conservation. Regional variation in climate change coupled with differential responses of species (due to time-lags in range-shift responses) would help contribute to the formation of novel biotic communities and ecosystems, which would accentuate trends anticipated to occur solely as an outcome of shifts in native species distributions (Hobbs et al. 2010). These accentuated alterations may further stress native species that are already imperiled by climate change, creating a double-risk for native species.

Acknowledgments We thank D. Currie, E. Fleishman, J. Lockwood, S. Norman, D. Richardson, and R. E. Ricklefs for helpful comments, and Jun Wen for advices on statistical analysis. This work is supported by NSF (DEB-0640058), the US Department of Agriculture (USDA), and Brown University.

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