

# Multiple mechanisms in woodland plant species invasion

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## Abstract

### Aims

A plethora of theories explain species invasion, yet when tested in isolation, support or falsification becomes contingent on study species, system and approach. Our objective was to examine community-level species invasion as a function of multiple competing hypotheses.

### Methods

We used data from >3500 woodland plant species in 2750 plots in 49 national parks in eastern US deciduous forests to test multiple competing theories of species invasion: competition, empty niche, propagule pressure and latitude matching. We also tested interactions with residence time to account for non-native species naturalization and spread since arrival.

### Important Findings

The non-native herbs generally thrived at latitudes similar to those from which they originated, but not necessarily where they were originally introduced to the eastern US. Overall, we found that each

hypothesis explained at least some aspect of woodland plant species invasion, but examining them simultaneously allowed assessment of their relative strengths and interactions. Our results suggested that residence time is a strong predictor of non-native woodland plant success, particularly as it interacts with other mechanisms of invasion, such as competition (abundance of native woodland plants), climate matching (similar invaded latitude as home range), propagule pressure (distance to putative seed sources) and empty niche (relatedness to native plants). We found that initial barriers, such as distance from propagule source or suboptimal habitat, were overcome, as was resistance from native relatives. However, the biggest challenge for the non-native woodland plants appeared to be time, as they declined after ~1 to 2 centuries.

**Keywords:** competition, empty niche, invasion biology, propagule pressure, latitude matching, residence time

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## INTRODUCTION

No single paradigm or theory proves satisfactory in explaining the success of translocated species in novel ranges. Proposed theories may be like the Indian fable involving a group of blind men describing an elephant, each sampling a different portion of the animal and describing its individual parts differently. That is, sampling different portions of the same animal might inspire very different descriptions based on what part of the animal is touched: a tusk like a spear, or a trunk like a snake, or a tail like a rope. Indeed, despite support for individual theories in species invasion, contradictory evidence suggests that the results often are contingent upon species and system (Broennimann *et al.* 2007; Daehler 2001; Diez *et al.* 2008; Felker-Quinn *et al.* 2013; Fridley *et al.* 2007; Gallagher

*et al.* 2010; Kennedy *et al.* 2002; Levine *et al.* 2004; Liu *et al.* 2006; Lonsdale 1999; Moles *et al.* 2012; Ordóñez *et al.* 2010). Hence, individual parts of the animal are well explained, but not the animal itself.

Given that some non-native species dominate ecosystems, presumably to the detriment of native species (Vilà *et al.* 2011), many invasion biology theories assume that non-native species out-compete native species ('competition'). Non-native species may have competitive/fitness advantages because they are less constrained by enemies, bring superior 'weapons,' rapidly evolve increased competitive abilities, or possess some combination of these that give them greater fitness than native species (Blossey *et al.* 1995; Callaway *et al.* 2004; Keane *et al.* 2002; van Kleunen *et al.* 2010). Darwin (1859) hypothesized that species invasion is an opportunistic enterprise in

which successful invaders arrive where native species do not fully utilize local resources so that there is little competition for those resources ('empty niche') (Stachowicz *et al.* 2005). Hence, established native species should resist invasions of taxonomically related invaders if closely related species compete for the same resources (Burns *et al.* 2011; Diez *et al.* 2008). Alternately, non-native species often increase with native species (Fridley *et al.* 2007; Liu *et al.* 2005; Lonsdale 1999; Stohlgren *et al.* 2005), suggesting that favorable habitats benefit both non-native and native species.

Longstanding observations of the association between non-native species and habitat alteration suggest that disrupting native communities makes them more 'invasible' (Chytrý *et al.* 2008; Davis *et al.* 2000; Elton 1958; MacDougall *et al.* 2005). Non-native species may better compete for the resources released with ecosystem disturbance than natives adapted to pre-disturbance conditions (Byers 2002; van Kleunen *et al.* 2011; Lamarque *et al.* 2013). Habitat disturbance also may create increased edge habitat which harbors non-native species with high fecundity that can overwhelm habitat and biotic limitations and allow establishment in otherwise marginal habitats ('propagule pressure') (Von Holle and Simberloff 2005; Warren *et al.* 2012).

Species niche requirements typically are conserved so that ecological traits remain static and evolution remains slow (Wiens *et al.* 2010)—even in novel habitats with high selection pressure (Anderson and Geber 2010). As a result, most non-native species likely die when they arrive in environments that do not meet their niche requirements (Holt *et al.* 2005). The degree of success in species invasion may simply reflect how pre-adapted the species is to the invaded habitat ('latitude matching') (Fridley 2013; Fridley *et al.* 2014). That is, successful non-native species may be those that are translocated into the novel ranges most like their home range (Wiens *et al.* 2005). An almost universal pattern is a lag between the arrival of a non-native species and any subsequent dominance (Chytrý *et al.* 2008; Crooks *et al.* 2001), which may reflect the plant's ability to disperse to suitable habitat at a different latitude from where it was introduced. However, it also might indicate the time it takes to rapidly evolve to the introduced habitat (Blossey and Notzold 1995).

Our objective was to examine community-level species invasion as a function of multiple competing hypotheses. That is, instead of a single null hypothesis, we test multiple hypotheses to determine the best model, or models, explaining the phenomenon (Chamberlin 1890; Platt 1964). We used data from 2752 plots in 49 eastern US National Parks to examine five competing hypotheses for non-native species invasion: competition, empty niche, disturbance/propagule pressure and latitude matching. We recognize that there are more theories for non-native invasion than those tested here, but we were limited by available data for such a large-scale analysis, and our main objective was integrating multiple hypotheses. We used interactions with the time since arrival (residence time) to account for the possibility that

non-native species 'naturalize' or rapidly evolve after arrival. The residence time also may reflect the degree of difference between the non-native species ancestral and novel habitat as it takes time to disperse to conserved habitats or adapt to novel ones (Blossey *et al.* 1995; Crooks *et al.* 2001; Holt *et al.* 2005). We assess the proxy parameters for each hypothesis in the same models to assess the impact of each predictor on non-native plant abundance and richness in the context of the other predictors.

## METHODS

### Data sources

The National Park Service (NPS) data includes 4952 plots that range in size from 25 to 1000 m<sup>2</sup>. The most common plot size was 20 × 20 m (400 m<sup>2</sup>). We chose to only use this plot size rather than standardize the other plots for parsimony. Native and non-native species abundance and richness were analyzed for herbaceous-layer plants in 2 752 400 m<sup>2</sup> plots located in 49 US National Parks in the eastern United States. These data were collected by NPS personnel in the late 1990s/early 2000s as part of a comprehensive US National Park Service Vegetation Inventory (USNPS 2014). The number of plots sampled varied with park area. Native and non-native species abundance ( $\Sigma$  plant cover (%) species type<sup>-1</sup> plot<sup>-1</sup>) and richness, plot location and litter cover were compiled from the NPS data. Latitude (median of the longitudinal range) of plant origin and year first recorded were compiled from several databases, mainly the US Department of Agriculture National Exotic Species Information Center and the US Forest Service Fire Effects Information (USDA 2014; USFS-FEIS 2014). Non-native plants with ambiguous ranges of origin, or ranges that spanned multiple continents or hemispheres, were omitted from analysis. Distance from road measurements were calculated using Google Earth Pro (Google 2014).

### Indicator variables

We used plot-level abundance of native plant species ( $\Sigma$ cover (%) native species<sup>-1</sup>) as an indicator of 'competition'. The 'empty niche' hypothesis suggests that closely related species require similar niche resources so that native plants should resist their non-native congeners. We estimated the impact of congener matches by calculating the proportion of the same genera between non-native (I) and native (N) congeners in each plot as a proportion of all (A) unique genera in that plot:  $\Sigma(G_I = G_N) / \Sigma G_A$ , where G = genus. Hence, our 'empty niche' variable is a measure of taxonomic relatedness between native and non-native plants in each plot with the assumption that fewer taxonomic matches indicates more unused niche resources, or 'empty niches'. We used distance from plot to road as the indicator variable for 'propagule pressure'. We chose this parameter because forest edges/roadsides are common non-native species reservoirs (Flory *et al.* 2009; Ulyshen *et al.* 2004; Warren *et al.* 2013) and distance to road/edge is a common propagule pressure proxy (Catford *et al.* 2011;

Chytrý et al. 2008). We used years since the non-native species was first recorded in the eastern US for ‘residence time’ and the difference between the plot latitude where the non-native plant was found in the USA and the median latitude of where it originated for ‘latitude matching’.

For an initial evaluation of the individual hypothesis proxies, we created quantile regression graphics for non-native species richness as a function of each hypothesis proxy with the fitted line at the 95<sup>th</sup> quantile. Ecological data often are messy with predictor values setting a limit captured by evaluating upper quantiles (Cade et al. 2003). That is, rather than tight-fitting residuals on a trendline, data might form a ‘wedge-shaped’ response driven by multiple contributions to variance. We graphed the data and fitted 95<sup>th</sup> percentile trendlines to verify the efficacy of the individual proxies before testing them in conjunction. For the graphic, we used the raw difference in latitude values for latitude matching to make interpretation straightforward, but we used the absolute values for statistical analysis.

### Data analysis

The non-native species abundance ( $\Sigma$ cover (%) non-native species<sup>-1</sup>) plot data essentially were count data, but Poisson error was highly overdispersed. Moreover, the data were skewed by zeros, which eliminates the possibility for effective transformation toward normality. The negative binomial error distribution is a good fit for overdispersed count data, and a zero-inflated model handles the excessive zeros. For these reasons, we used a zero-inflated mixed model (ZIMM) assuming a negative binomial error distribution to evaluate non-native species abundance as a function of native species abundance (‘competition’), congener matches (‘empty niche’), distance to road (‘propagule pressure’), latitude difference (‘latitude matching’) and time since first recorded (‘residence time’). We note that because plant cover (native and non-native) was a sum of plot coverage for individual of each type, the abundance variables were not constrained (plot cover could, and did, exceed 100 due to plant layering). The ZIMM was evaluated using the (‘glmmADMB’) package (Fournier et al. 2012) in the R statistical program (R Core Team 2016). Because the data were clustered by US National Park, we included park ( $n = 49$ ) as a random effect to account for potential autocorrelation. Potential collinearity between predictor variables was evaluated using variance inflation factors generated in the (‘car’) package (Fox et al. 2011). The variance inflation factors for the predictor variables in all were <1.5, indicating they independently predicted variance, and overdispersion was <1.1 in the ZIMM model. We included second-order terms to examine non-linear responses, and we included interaction terms for residence time  $\times$  the other predictor variables, but removed them if not statistically significant. We used standardized coefficients to plot significant continuous interaction effects.

Given the species richness data were discrete counts, we used a generalized linear mixed model (GLMM) with a

Poisson error distribution to evaluate non-native species richness with the same fixed effects as the abundance model. The GLMM was evaluated using the (‘lme4’) package (Bates et al. 2015) with park as a random effect. The species richness data were not collinear or overdispersed. We included the same interaction and second-order terms as the abundance model. We used standardized coefficients to plot significant continuous interaction effects.

All statistical analyses were conducted using the R statistical program (R Core Team Version 3.3.2 2016). We considered coefficients with  $P$  value <0.05 significant and coefficients with  $P$  value <0.10 marginally significant.

## RESULTS AND DISCUSSION

The plots used for this study contained herbs, shrubs and trees of 3537 species, 254 of which were non-native. Our focus was the herbaceous layer, which contained 3277 species—the vast majority of deciduous forest richness (Gilliam 2007)—and all of the non-native species. The most common native plant species, by frequency of plots found, all were shade-tolerant perennials, and all forbs except one graminoid (Table 1a). The most common non-native plants were mostly shade-tolerant perennial forbs (Table 1b). The top three most common non-native plants in the herbaceous layer—*Alliaria petiolata* (garlic mustard), *Microstegium vimineum* (Nepalese browntop) and *Berberis thunbergii* (Japanese barberry)—include a graminoid, shrub and forb, and are very well known non-native invaders in the eastern US. We note that these are woodland herbaceous species that are vigorous forest invaders that can dominate habitats and suppress other plant species, including trees (Eschtruth et al. 2009; Morrison et al. 2007; Warren et al. 2011).

The 95<sup>th</sup> quantile regression graphics suggested that each hypothesis proxy individually corresponded with variation in non-native species richness (Fig. 1). Mean ( $\pm$ standard error) non-native richness was highest at intermediate levels of native species (Fig. 1a), latitude difference (Fig. 1b) and residence time (Fig. 1c), and it declined with increased distance to road (Fig. 1d) and congener match (Fig. 1e).

A significant non-linear response in the ZIMM indicated that non-native species abundance peaked where the invaded-range plants occurred at intermediate differences from their latitude of origin (Table 2; Fig. 2a); that is, they were most abundant at latitudes most similar to  $\sim 5$  to  $10^\circ$  north of their latitude of origin. A significant interaction term indicated that non-native species abundance increased with residence time and decreased with distance to road, but decreased less with greater distance to road with longer residence time (Table 2; Fig. 2b). A second significant interaction term also indicated that non-native species abundance decreased with shared congeners and increased with residence time, but increased even more with longer residence time and shared congeners (Table 2; Fig. 2c). Native species abundance did not have a statistically significant impact on non-native species abundance in the ZIMM model.

**Table 1:** the 10 most common herbaceous-layer native (a) and non-native (b) plants (by plot frequency;  $n = 2750$  total) in eastern deciduous US National Park forests

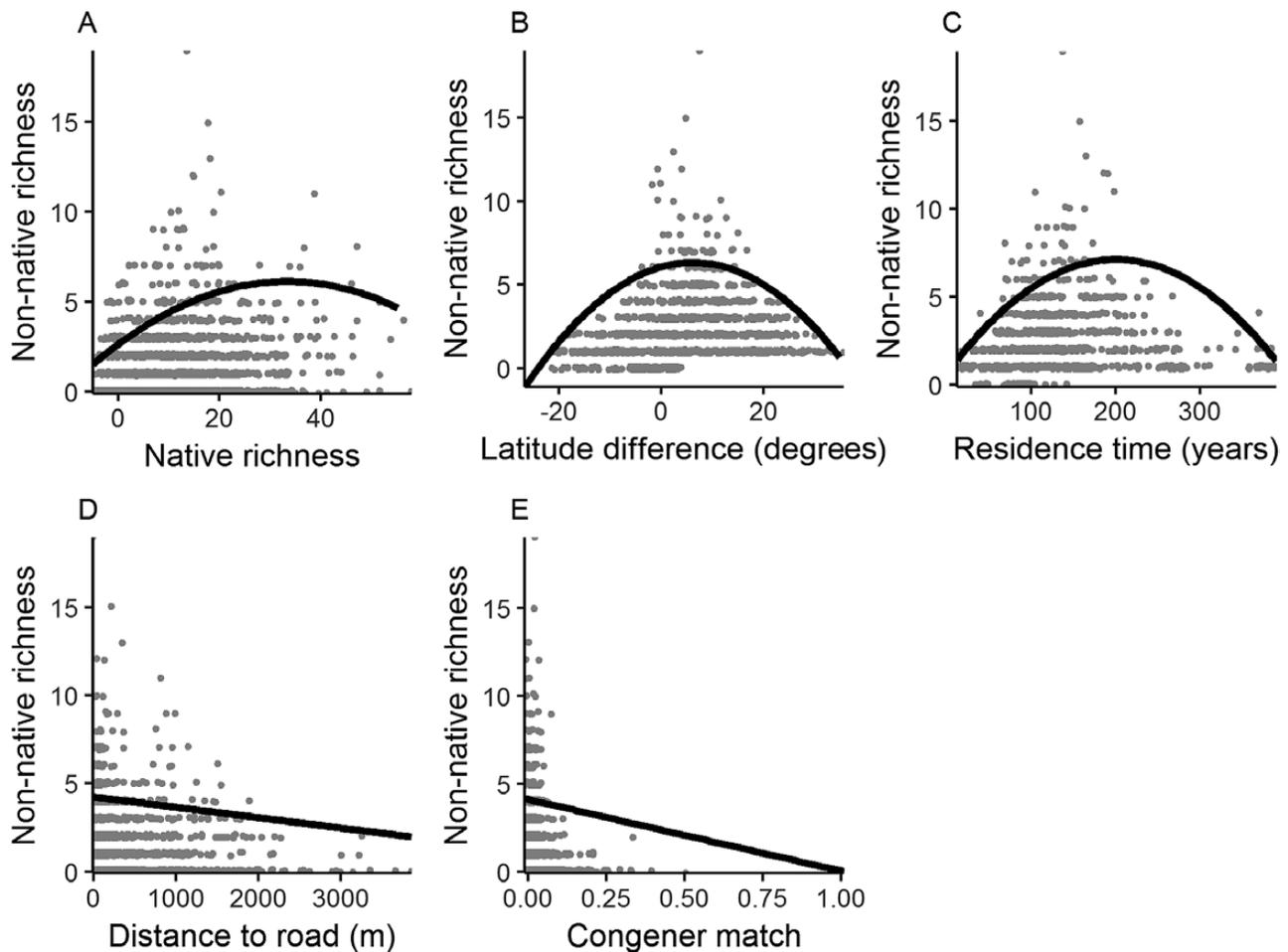
Taxon	Common	Plots	Life history	Habit
a) Native plants				
<i>Arisaema triphyllum</i> (L.) Schott	Jack in the pulpit	596	Perennial	Forb
<i>Maianthemum canadense</i> Desf.	Canada mayflower	549	Perennial	Forb
<i>Eurybia divaricata</i> (L.) G.L. Nesom	White wood aster	491	Perennial	Forb
<i>Galium triflorum</i> Michx.	Fragrant bedstraw	461	Perennial	Forb
<i>Maianthemum racemosum</i> (L.) Link	False lily of the valley	438	Perennial	Forb
<i>Mitchella repens</i> L.	Partridgeberry	402	Perennial	Forb
<i>Galium circaezans</i> Michx.	Licorice bedstraw	323	Perennial	Forb
<i>Carex pensylvanica</i> Lam.	Pennsylvania sedge	319	Perennial	Graminoid
<i>Circaea lutetiana</i> L.	Broadleaf nightshade	316	Perennial	Forb
<i>Trientalis borealis</i> Raf.	Starflower	290	Perennial	Forb
b) Non-native plants				
<i>Alliaria petiolata</i> (M. Bieb.) Cavara & Grande	Garlic mustard	324	Biennial	Forb
<i>Microstegium vimineum</i> (Trin.) A. Camus	Nepalese browntop	242	Annual	Graminoid
<i>Berberis thunbergii</i> DC.	Japanese barberry	217	Perennial	Shrub
<i>Polygonum caespitosum</i> Blume, nom. inq.	Oriental lady's thumb	147	Annual	Forb
<i>Glechoma hederacea</i> L.	Ground ivy	115	Perennial	Forb
<i>Poa compressa</i> L.	Canada bluegrass	81	Perennial	Graminoid
<i>Veronica officinalis</i> L.	Common gypsyweed	77	Perennial	Forb
<i>Polygonum scandens</i> L.	False buckwheat	63	Perennial	Forb
<i>Poa pratensis</i> L.	Kentucky bluegrass	59	Perennial	Graminoid
<i>Allium vineale</i> L.	Wild garlic	53	Perennial	Forb

A significant non-linear response in the GLMM indicated that non-native species richness peaked at intermediate levels of native species abundance (Table 3; Fig. 3a) and decreased significantly with distance to the nearest roadway (Table 3; Fig. 3b). A significant interaction term indicated that non-native species richness increased with residence time and decreased with latitude difference, but decreased even more with the longest residence times and latitudinal distances (Table 3; Fig. 3c). Shared congeners did not have a statistically significant impact on non-native species richness in the GLMM model.

Each hypothesis explained at least some aspect of woodland plant species invasion, but examining them simultaneously allowed assessment of their relative strengths and interactions. In the end, these results suggested that the non-native plants thrived in climate conditions similar to those in which they evolved (latitude matching), and after establishment and spread, they declined with time—a decline that is particularly pronounced at the latitudes most different from where they originated. In the US National Park forests, non-native woodland plant abundance and richness declines with distance from the nearest road, but forest interior abundance eventually increased for those with the longest residence time (time since first reported in the invaded range). Native woodland plants appeared to pose little resistance for the non-natives, although non-natives were less invasive in plots containing

closely related native plants (empty niche)—native resistance also declined with residence time. Successful non-native species may be those that possess both the plasticity to persist in suboptimal habitat and the dispersal abilities (either inherent or anthropogenically assisted) to eventually reach optimal habitat.

The non-native plants observed here appeared niche conserved as their highest abundance and diversity at invaded latitudes generally matched their latitude of origin, presumably because climates and other environmental limits at equivalent latitudes are similar (Broennimann *et al.* 2007). These patterns appeared influenced by their residence time, as non-native species diversity declined more the longer they inhabited latitudes that poorly matched their latitudes of origin. The median latitude of origin for the non-native species peaked at  $\sim 34^\circ$  north, which crosses through North Africa, southern Europe and southern Asia, including China and Japan. However, in the USA, the non-native species appeared most abundant at latitudes  $\sim 5$  to  $10^\circ$  north of where they originated,  $\sim 39^\circ$  north latitude in the eastern US, which is mid-continental, approximately through the states of Kentucky, West Virginia and Virginia. Given that 1879 is the mean year that these non-native herbs were first recorded in the USA, the bias toward northern latitudes may reflect that most US commerce and agriculture import was conducted in the Northeast and Great Lakes regions at that time. With time,



**Figure 1:** data corresponding with variation in non-native plant species richness in US National Park forest plots. Shown are 95<sup>th</sup> quantile regression plots of non-native species richness with native species richness (a), the difference in latitude between the species' origin and invaded plot (b), the residence time since the non-native was first reported in the USA (c), the distance to the nearest road (d) and the proportion of congener matches between native and non-native plants in each plot (e).

it appears that the non-native species dispersed toward more southerly latitudes as many species were extirpated where the latitude match was poorest.

Conserved niche requirements would benefit the plants if they arrive in habitat where those resources are underutilized by the established native plants, i.e., 'empty niches'. Otherwise, taxonomically similar native plants should resist invasion (Darwin 1859; Elton 1958). We analyzed how the percentage of congener matches between non-native and native species impacted non-native presence and abundance; we found non-native abundance decreased with congener matches, suggesting that the non-native species benefited from empty niches, though that benefit declined with time, suggesting that the non-native species displaced natives from occupied niches. Competition anchors several theories of species invasion (Blossey et al. 1995; Callaway et al. 2004; Keane et al. 2002; van Kleunen et al. 2010). For example, Levine et al. (2003) found that, of 150 studies looking at impacts of non-native plant species, almost

all reported non-native species as competitively superior to native species. Similarly, reviews performed by Vila et al. (2004) and Gioria et al. (2014) also reported that non-native plants often appear to be better competitors than native plants (but see Warren et al. 2017). Levine et al. (2004) concluded that native species fail to prevent non-native species invasion but do constrain their abundance. Non-native species richness was highest in plots contained intermediate abundance of native species, possibly a mixed effect of native resistance and a shared affinity for similar resources.

Niche and fitness differences between native and non-native species may determine the success of non-native invaders (Chesson 2000; MacDougall et al. 2009). Successful establishment by non-native species depends on the non-native species either having a fitness advantage to out-compete native species (directly or through better exploitation of resources) or a distinct niche requirement different enough from the native species to allow it to flourish without

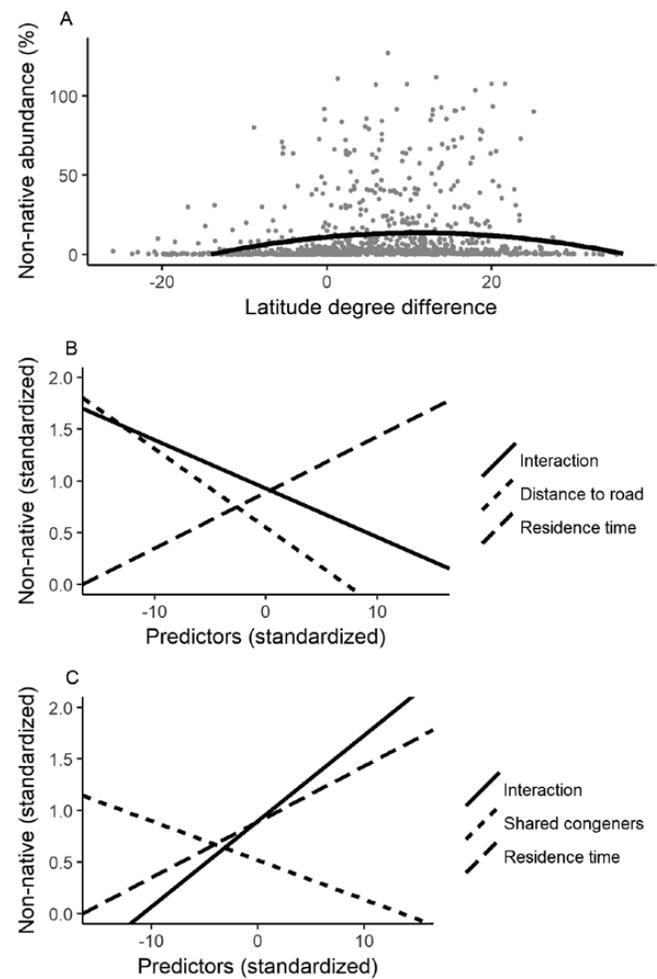
**Table 2:** standardized coefficients for zero-inflated mixed model of non-native species abundance ( $\Sigma\text{cover} (\%) \text{species}^{-1}$ ) assuming a negative binomial error distribution

Coefficient	Coeff.	SE	t value	P value
Native species abundance	0.004	0.003	1.300	0.194
Native species abundance <sup>2</sup>	0.001	0.001	0.380	0.703
Distance to road	0.001	0.001	3.830	<0.001
Latitude difference	0.055	0.056	9.830	<0.001
Latitude difference <sup>2</sup>	-0.002	0.001	-7.600	<0.001
Residence time	0.008	0.002	3.920	<0.001
Residence time <sup>2</sup>	0.001	0.001	-1.670	0.095
Shared congeners	-1.753	3.422	-0.510	0.608
Residence time $\times$ distance to road	-0.001	0.001	-3.850	<0.001
Residence time $\times$ shared congeners	0.038	0.020	1.940	0.052

The coefficients represent the average slope value across all random intercepts. *SE* = standard error.

competition (Chesson 2000). MacDougall *et al.* (2009) suggest that only a fitness advantage, however, allows a non-native species to dominate. Our results support MacDougall *et al.*'s (2009) conclusion as finding habitat in the invaded range that matched the conserved home-range niche was important for non-native plant species, but the invaded-range niche did not need to be 'empty.' Hence, invasion success appeared more linked to fitness advantages. Several hypotheses suggest mechanisms for the fitness advantages observed here. Native plants may be burdened by pathogens and herbivores that are not evolved to attack invaders (enemy release, Keane *et al.* 2002); the invaders may bring competitive traits against which native species have not coevolved (novel weapons, Callaway *et al.* 2004); rapid evolution may give the non-native species greater competitive abilities (evolution of increased competitive ability, Bossdorf *et al.* 2005) and the non-native species may exhibit greater plasticity and hence acclimation to novel conditions (Lamarque *et al.* 2013; Shea *et al.* 2002). We found both non-native abundance and richness bounded by residence time, peaking ~150 to 200 years after being first detected and then declining, similar to results reported for invasive plants in Spain (Gasso *et al.* 2009). That the plants appear to arrive in habitats dissimilar to those in which they evolved, and move toward their conserved niche requirements with time, suggests some level of plasticity in the surviving non-native plants and/or strong dispersal abilities.

Propagule pressure often is treated as a confounding variable, a consequence of non-native species proximity, land use or human activities, rather than an invasion trait itself (e.g., Thompson 2014). Propagule pressure undoubtedly is an important variable in species invasion (Colautti *et al.* 2006; Eschtruth *et al.* 2009; Warren *et al.* 2012, 2013). Our results suggested that non-native species abundance and richness declined with distance from roads, though the decline in abundance is ameliorated by residence time. These results suggest that fewer non-native species become established



**Figure 2:** non-native plant abundance ( $\Sigma\text{cover} (\%) \text{species}^{-1}$ ) in US National Park plots as a function of the difference in latitude between the species' origin and invaded plot (a), continuous interaction between years since first reported in the USA (residence time)  $\times$  distance to nearest road (b) and continuous interaction between residence time  $\times$  proportion of non-native and native plants in the same genera (shared congeners) (c).

further from roads, possibly the best dispersers. Given that the most common non-native species investigated here are adapted to forest understory conditions, these results suggest that propagule pressure from road edges may introduce species that do not otherwise thrive in forest understories, and higher quality interior forest habitat favored those that do, such as *M. vimineum*, *A. petiolate* and *B. thunbergii* (see online supplementary Fig. S1; Eschtruth *et al.* 2009). Given that disturbance is such a strong driver of species invasion, any propagule pressure proxies based on land use parameters are themselves confounded, and propagule pressure itself can be a syndrome of traits, including seed size, reproductive output and dispersal distance—all of which are controlled by habitat conditions.

Our propagule pressure proxy, distance to roads, also may act as a proxy for forest disturbance. The mechanism by

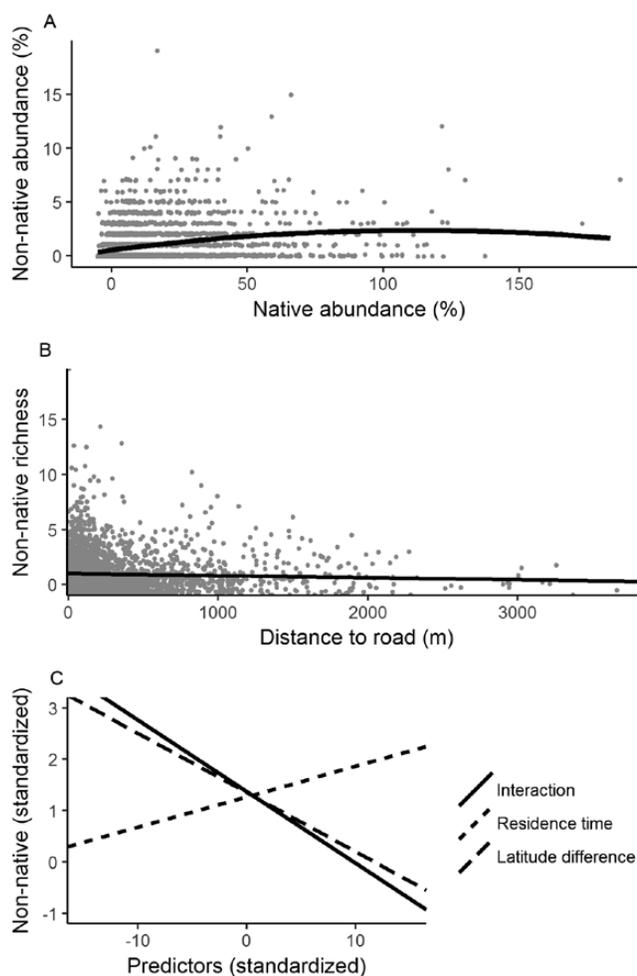
**Table 3:** standardized coefficients for generalized linear mixed model of non-native species richness assuming a Poisson error distribution

Coefficient	Coeff.	SE	z value	P value
Native species abundance	0.184	0.032	5.739	<0.001
Native species abundance <sup>2</sup>	-0.018	0.006	-2.726	0.006
Distance to road	-0.078	0.025	-3.114	0.001
Latitude difference	-0.027	0.027	-0.987	0.323
Latitude difference <sup>2</sup>	-0.124	0.023	-5.399	<0.001
Residence time	0.255	0.033	6.660	<0.001
Residence time <sup>2</sup>	-0.110	0.018	-6.130	<0.001
Shared congeners	0.019	0.063	0.315	0.752
Residence time × latitude difference	-0.230	0.032	-7.064	<0.001

The coefficients represent the average slope value across all random intercepts. *SE* = standard error.

which higher biodiversity creates invasion barriers (Kennedy et al. 2002) might not be an inherent function of species as much as a reflection of unaltered habitat. That is, one expects a correspondence between native species diversity and unaltered native habitat, and hence better competitive abilities of native species adapted to native habitat. It may not be that diversity resists invasion as much as unaltered habitat does. Ecologists long ago noticed that non-native species thrive in anthropogenically altered habitats (Elton 1958)—a habitat type increasing at a worldwide scale (Williams et al. 2007)—and current research verifies that non-native species favor anthropogenic/novel habitat (King et al. 2008; MacDougall et al. 2005). A longstanding belief is that non-native species are pre-adapted to early successional habitats so that they thrive in anthropogenically altered conditions, which gives them competitive advantage against native species (van Kleunen et al. 2011; Lamarque et al. 2013). Novel habitat may select for non-native species with pre-adaptations for that habitat or the plasticity to acclimate to different conditions (novel niche, Shea et al. 2002), and habitat disturbance may knock back native species and open up resources for invading species (fluctuating resources, Davis et al. 2000).

Residence time appears a core part of invasion that interacts with other mechanisms, such as climate matching, propagule pressure and empty niche. Initially, time appears to benefit non-native species as they establish in a novel range. They likely face low enemy loads, and any successful dispersal increases their populations and invaded range. As they spread, initial barriers, such as distance or suboptimal habitat, were overcome, as was resistance from native relatives. However, their biggest challenge appeared to be time, as they all declined after ~1 to 2 centuries, suggesting that pathogens and herbivores caught up with them. These results suggest that non-native species thrive in climate conditions that match the climate in which they evolved, and they displace native species from those conditions. With



**Figure 3:** non-native plant species richness in US National Park plots as a function of native plant abundance (a) distance to the nearest road (b) and continuous interaction between years since first reported in the USA (residence time) × distance between home range and invaded latitude (latitude difference) (c).

time, however, non-native abundance and richness decline, most rapidly at latitudes most dissimilar from their origins, likely from the same ecological constraints that limit native species.

## SUPPLEMENTARY DATA

Supplementary material is available at *Journal of Plant Ecology* online.

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## DATA ACCESSIBILITY

All the data contained in this manuscript are publicly available with sources given in the Methods and References.

*Conflict of interest statement.* None declared.

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