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BIODIVERSITY RESEARCH

Divergent biogeography of native and introduced soil macroinvertebrates in North America north of Mexico

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ABSTRACT

To improve understanding of the biogeographical consequences of species introduction, we examined whether introduced soil macroinvertebrates differ from natives in the relationship between species richness and key environmental predictors, and whether such differences affect the relationship between native and introduced species richness. For North America north of Mexico, we summarized jurisdiction occurrence data for seven macroinvertebrate taxa with strong influences on soil biodiversity or processes. We analysed the relationships of native and introduced species richness to each other using linear regression; to latitude using Gaussian regressions; and, using the residuals of the richness–latitude regressions, to distance from coasts, human population density, and human population size using regression and correlation. We found weak to strong positive relationships between native and introduced species richness. This variation was related to divergent relationships of native and introduced species with latitude, human population density, and distance from coasts. Native species richness declined with increasing latitude for all taxa, as did introduced species richness for taxa with predominantly lower-latitude origins (ants, termites, non-lumbricid earthworms). In contrast, introduced species richness peaked at higher latitudes for four taxa of predominantly Palearctic origins (weevils, ground beetles, lumbricid earthworms, isopods). Partitioning introduced taxa within these groups based on region of origin, we found that Palearctic taxa were distributed at higher latitudes than non-Palearctic taxa. Thus source region appears to strongly influence introduced species richness–latitude relationships. Compared to natives, introduced species exhibited more positive relationships with human population density and negative relationships with distance from coasts, but did not differ in relationships with human population size. Thus coastal, densely populated regions are likely to have a higher proportion of introduced soil macroinvertebrate species. These differences between distribution of native and introduced species tend to weaken positive correlations between native and introduced species richness, especially for taxa dominated by Palearctic introductions.

Keywords

Biological invasions, Carabidae, Curculionidae, distance from coasts, Formicidae, human population density, Isopoda, Isoptera, latitude–species richness relationships, Oligochaeta.

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INTRODUCTION

Despite concerns about the effects of invasive species on biodiversity and ecosystems (McKinney & Lockwood, 1999; Crooks, 2002) our understanding of the large-scale biogeographical consequences of species introductions is limited. Yet such understanding is essential both as a test of biogeographical theory and to inform proactive strategies addressing invasive species. Although some attention has been paid to the biogeography of introduced plants, vertebrates, and phytophagous insects (e.g. Niemalä & Mattson, 1996; Lonsdale, 1999; Stohlgren *et al*., 1999; Sax, 2001; Sax & Gaines, 2006), we have a poor understanding of the biogeography of introduced soil macroinvertebrates. Soil macroinvertebrates regulate ecosystem processes such as nutrient and carbon cycling, hydrological fluxes, decomposition and soil formation, erosion and bioturbation (Van der Putten *et al*., 2001; Setälä, 2002; Wardle *et al*., 2004). Therefore, changes in their biogeography could cause dramatic shifts in these processes,

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especially in the case of introduced 'ecosystem engineers' such as ants (Formicidae), termites (Isoptera), and earthworms (Oligochaeta) (Hooper *et al.*, 2000).

In addition, no taxonomic group has been explicitly examined to assess whether the relationship of species richness with key predictors variables (e.g. latitude, distance from coasts, and human population density) differs between native and introduced species. Examination of these patterns for multiple taxa will inform our fundamental understanding of the factors that generate biogeographical patterns. We hope that this information will also contribute to efforts to improve our ability to predict, prevent, and respond to species invasions.

We asked two related questions: do both native species richness (NSR) and introduced species richness (ISR) exhibit the same relationship with environmental predictors, and what is the relationship between NSR and ISR at the scale examined? Whether positive, negative, or no relationships between NSR and ISR will develop depends on three things: the universality of dominant abiotic controls on biogeographical patterns; the strength and sign of any biotic interactions between NSR and ISR; and the influence of points of introduction, rates of spread, and regions of origin on distribution of introduced species. Positive relationships between NSR and ISR could arise if both respond in the same way to environmental factors (e.g. Stohlgren *et al.*, 1999; Gilbert & Lechowicz, 2005), e.g. if both groups exhibit negative relationships between richness and latitude or positive relationships with productivity. Negative species richness–latitude relationships predominate (Willig *et al.*, 2003; Hillebrand, 2004) and might be expected to develop in both native and introduced members of the same taxa (Sax & Gaines, 2006).

A second possibility is that NSR and ISR might be negatively correlated. This could occur as a result of biotic resistance by native species, which might be important at local scales (Levine *et al.*, 2004). However, biotic resistance appears to be less important at larger spatial scales where positive associations of native and introduced species richness seem to predominate (Lonsdale, 1999; Stohlgren *et al.*, 1999, 2005; Sax & Gaines, 2006; and references therein).

A third possibility is that the relationship between NSR and ISR, and the relationship of both NSR and ISR to environmental predictors might vary among taxonomic groups. One cause of such a divergence among taxa would be if native species exhibit consistent relationships with latitude, while introduced species do not because of differences among taxa in points of species introduction, probability of survival at different points of introduction, or rates of spread (Pyšek, 1998; Blackburn & Duncan, 2001). Region of origin of introduced species could have a dominant influence on introduction success at different latitudes and resultant biogeographical patterns, because of the match between abiotic conditions in the source and colonized regions (Blackburn & Duncan, 2001). For example, taxonomic groups introduced mainly from lower-latitude sources might be more likely to exhibit negative richness–latitude relationships than taxa from higher latitudes sources.

In addition, distributions of introduced taxa might be likely to diverge from those of natives because of the strong influence of human patterns of propagule dispersal and habitat modifications on current species distributions. Thus, differing relationships with predictors of human activity (e.g. population size or density) and likely hotspots of introduction (e.g. coastlines) could lead to divergent distributions of native and introduced species, weakening any patterns driven by positive relationships with abiotic gradients.

In order to test the above alternatives, we summarized continental jurisdiction (i.e. US state plus District of Columbia, and Canadian province and territory) species occurrence data for the following diverse taxonomic groups containing important soil- or litter-dwelling invertebrates: Oligochaeta (earthworms – as a whole, and divided into Lumbricidae and non-Lumbricidae), Isopoda (wood lice), Carabidae (ground beetles), Curculionidae (weevils), Isoptera (termites), and Formicidae (ants). We examined the relationships between ISR and NSR, as well as the relationship of ISR and NSR with latitude, distance from coasts, human population size, and human population density of the jurisdiction.

METHODS

Data sources

We used published sources to determine jurisdiction (US state and district, Canadian province and territory) occurrence data for Oligochaeta (Reynolds & Wetzel, 2004), Isopoda (Jass & Klausmeier, 2000, 2001), Carabidae (Bousquet & Larochelle, 1993), Curculionidae (O'Brien & Wibmer, 1982), Isoptera (Weesner, 1970; Messenger, 2003; T. Myles, personal communication), and Formicidae (Nielsen, 1987; Wheeler & Wheeler, 1988; Wheeler *et al.*, 1989, 1994; Francoeur, 1997; Naumann *et al.*, 1999; O'Keefe *et al.*, 2000; Mackay & Mackay, 2002; Deyrup, 2003; Dash, 2004; Ward, 2005; Ivanov, 2007; MacGown, 2007; Trager & Rericha, 2007; Trager, 2007; S. Cover, unpublished). Studies used for Oligochaeta, Isopoda, Carabidae, and Curculionidae were compilations by single authors, so all nomenclature issues were resolved by those authors. For two taxa (Isoptera and Formicidae) multiple sources were used. In the case of Isoptera three sources covering North America north of Mexico (NANM) were combined (Weesner, 1970; Messenger, 2003; T. Myles, personal communication). In the case of Formicidae, separate sources for 21 jurisdictions were combined, because there is no monographic treatment of the distribution of this group in North America. To minimize differences among sources in nomenclature and temporal effects on reported introduced ant species richness, we chose state, province, and territory lists compiled since 1987. Nomenclature for introduced ants followed Bolton (1995); except for *Pyramica*, we followed Bolton (2000). We used the number of native and introduced species as defined by the authors of the list, after correcting for any inconsistency among studies in assignment of species to native versus introduced status. If a species' introduced status was uncertain it was included in the native species pool.

We included all terrestrial species listed for the taxonomic groups in NANM, except in the case of Isopoda we selected only non-cave, non-littoral species for analysis. Unless noted, sample size (n) of jurisdictions for all analyses was 62, except for Formicidae, where data for 21 US and Canadian jurisdictions fit our criteria.

Several taxa exhibited distinct high-latitude peaks of ISR. To determine whether these deviations of ISR– from NSR–latitude relationships were related to the geographical and bioclimatic source region for those species, we examined three taxa for which source information was available (Oligochaeta, Curculionidae, Carabidae) in more detail. Using published literature sources, we identified the native range for all of the introduced species in these taxa. We divided these native ranges into Palearctic and non-Palearctic categories. For Oligochaeta, all Palearctic species were Lumbricidae; non-Palearctic taxa were predominantly Megascolecoidea (Reynolds & Wetzel, 2004) mostly of Asian origin with a subtropical to tropical centre of diversity in their native ranges (Edwards & Lofty, 1972). For Curculionidae, Palearctic taxa were predominantly Eurosiberian; non-Palearctic taxa were of diverse origins, including South American, broad-ranged Eurasian, Japanese, Caribbean, Philippine, and Australian taxa. For the introduced Curculionidae, the initial analyses included all Curculionidae, not just root feeders, because of the difficulty of identifying root-feeding status for the entire data set. However, for the analysis of the effect of geographical origins on richness–latitude relationships, we examined the subset of the introduced Curculionidae that from the literature we determined had a root-feeding life stage. For Carabidae, Palearctic taxa all had broad ranges including Europe, sometimes northern Asia, and occasionally extending into North Africa or central Asia; non-Palearctic taxa were of diverse origins.

For each jurisdiction, values of five predictor variables were determined: latitude of geographical centre, distance from coasts to nearest border, human population size and density from the 1990 census, and area. For distance from coasts, calculations were performed both with and without the five Great Lakes included as sources of coastline. The Great Lakes have been important in shipping, so are potential points of entry for introduced species.

Statistical analyses

Linear and nonlinear regressions, correlations, and curve-fitting were performed in Sigmaplot version 9.01 or SPSS 13.0 (SPSS Inc., Chicago, IL, USA). For all regressions, tests were carried out for correlation of residuals (Durbin–Watson test), and normality (the Kolmogorov–Smirnov test).

Controlling for effects of area

We examined the richness data for possible confounding effects of area by regressing richness against area for both native and introduced species. As no positive richness–area relationships were found, we did not attempt to remove the effects of area before further analysis. To determine whether area effects could be discerned after controlling for the effect of latitude, we examined the residuals of richness–latitude regressions for relationships with area (see below).

Richness–latitude relationships

For each state or province, we regressed latitude of geographical centre against ISR and NSR. To examine the species richness–latitude data for possible peaks of richness, we performed nonlinear regressions with three parameter Gaussian fits for the relationship of $\log_{10}$(species richness + 1) with latitude. We also fit the most appropriate linear or nonlinear relationship to percentage of introduced species versus latitude.

Effect of region of origin on richness–latitude relationships

For all three taxa, we compared the ISR–latitude relationships of Palearctic and non-Palearctic species in NANM. For Oligochaeta, we also determined their richness–latitude relationships in Europe from data in Judas (1988) which we compared with ISR–latitude relationships for Palearctic and non-Palearctic Oligochaeta in NANM.

Effects of population density, distance from coasts, and area

To remove the dominant effect of latitude on species richness in analyses of effects of human population size, population density, and area, we regressed $\log_{10}$ population size, $\log_{10}$ population density, and $\log_{10}$ area against the residuals of the Gaussian regression of $\log_{10}$(species richness + 1) versus latitude. In the case of area, we were not interested in defining area effects on species richness *per se*, but rather in testing for any possible confounding effects of area of jurisdiction on the other analyses. For analyses of the effect of distance from coasts on richness, we performed Spearman correlations with the same residuals as above, because violations of normal distribution assumptions for the distance data precluded use of least squares regression. To test for differences between ISR and NSR in the slopes, r^2, and rho for the above regressions and correlations, we carried out paired *t*-tests or Wilcoxon signed-rank tests (as appropriate) for all taxa ($n = 7$) in SPSS 13.0. As we included Lumbricidae and non-Lumbricidae in the tests, Oligochaeta were not independent and so were excluded from these analyses.

Relationship of native and introduces species richness

We examined the linear regression of NSR versus ISR ($\log_{10}$-transformed to improve normality of the residuals). We only included jurisdictions where at least one native or introduced species was present. In addition, to examine the effects of latitude on this relationship we also performed the same regression analysis on the residuals of the log-richness–latitude relationships.

RESULTS

Controlling for species–area effects

One concern with our approach could be that we are comparing jurisdictions (states, districts, provinces, and territories) of differing area, so our results might be confounded by species–

Table 1 Effect of distance from coasts on species richness for native and introduced species in eight taxonomic groups of macroinvertebrates. Spearman correlations (rho) of the residuals of the richness–latitude regressions (from Fig. 1) with distance from coasts for both native species richness (NSR) and introduced species richness (ISR) for eight taxonomic groups of macroinvertebrates. Data are presented for correlations with and without the inclusion of the Great Lakes as coastline. *P*-values in parentheses.

	Spearman correlation (rho) not including Great Lakes		Spearman correlation (rho) including Great Lakes	
Taxon	Native	Introduced	Native	Introduced
Oligochaeta	−0.10 (0.43)	−0.47 (< 0.001)	−0.18 (0.06)	−0.43 (< 0.001)
Lumbricidae	−0.09 (0.50)	−0.39 (0.002)	−0.21 (0.11)	−0.35 (0.006)
Non-lumbricid Oligochaeta	−0.07 (0.58)	−0.27 (0.04)	−0.30 (0.02)	−0.227 (0.08)
Isopoda	−0.22 (0.08)	−0.13 (0.33)	−0.41 (0.001)	−0.31 (0.01)
Isoptera	0.11 (0.40)	−0.32 (0.01)	0.045 (0.73)	−0.44 (< 0.001)
Formicidae	−0.20 (0.38)	−0.18 (0.44)	−0.13 (0.58)	−0.40 (0.07)
Carabidae	−0.08 (0.53)	−0.62 (< 0.001)	−0.28 (0.03)	−0.67 (< 0.001)
Curculionidae	0.10 (0.45)	−0.364 (0.004)	−0.05 (0.73)	−0.40 (0.001)

area effects. However, before correcting for latitude there were no significant positive richness–area relationships for either native or introduced species, and in fact some significant negative relationships were found (data not shown), presumably driven by larger Canadian and US jurisdictions in the north where richness is low. Given this confound and the lack of any positive relationships, we considered it inappropriate to use a correction for area before examining richness–latitude relationships. After correcting for the effects of latitude (see below), area of jurisdictions was positively related to NSR for only three taxa (Isoptera, $r^2 = 0.14$; $P = 0.002$; Formicidae $r^2 = 0.36$, $P = 0.02$; Carabidae $r^2 = 0.11$, $P = 0.005$) and not to ISR of any taxon ($P > 0.05$ for all taxa), indicating that at the scales examined, area had minimal impact on the observed ISR patterns.

Richness–latitude relationships

For all taxa, NSR declined with increasing latitude; however, taxa differed in the relationship between ISR and latitude (Fig. 1). Only the Isoptera, Formicidae, and non-lumbricid Oligochaeta (all predominantly of subtropical to tropical origin) exhibited monotonic decline of ISR with latitude. Oligochaeta, Isopoda, Curculionidae, Lumbricidae, and Carabidae all exhibited convex relationships of ISR with latitude that peaked at 37, 39, 42, 46, and 49° N latitude, respectively (Fig. 1).

To test the hypothesis that these patterns were generated by the geographical origin of taxa, we compared ISR of Palearctic and non-Palearctic taxa in the Oligochaeta, Curculionidae, and Carabidae. For the Oligochaeta, ISR of Palearctic taxa in NANM and species richness of Oligochaeta in Europe both had convex relationships that peaked at *c.* 46 and 44 degrees, respectively (Fig. 2a). In contrast, ISR of non-Palearctic taxa in NANM declined monotonically with latitude (Fig. 2a). For both Curculionidae and Carabidae, ISR for taxa originating in the Palearctic peaked at higher latitudes (46° and 49°, respectively), whereas ISR for taxa that did not originate in the Palearctic declined with increasing latitude (Fig. 2b,c).

The net effect of species introductions on the shape of total (native + introduced) richness–latitude relationships is substantial for the Oligochaeta (mostly mediated by introduced Lumbricidae) and the Isopoda, but less so for other taxa because of numerical dominance by natives (Fig. 1).

Richness versus distance from coasts and human population density

After we statistically removed latitudinal effects, ISR was negatively correlated with distance from the coast for all taxa; in contrast, NSR was less negatively correlated with distance from the coasts most taxa, and was positively correlated with distance from coast for some taxa (Table 1). These patterns held whether or not the Great Lakes coasts were characterized as coastline. For all taxa taken together, this resulted in significantly stronger negative correlations with distance from coasts for ISR (mean ± standard error (SE): -0.40 ± 0.05 with Great Lakes included [+ GL] and -0.32 ± 0.06 without Great Lakes included [– GL]) than NSR (-0.19 ± 0.06 [+ GL] and -0.07 ± 0.05 [– GL]; paired *t*-test, $P = 0.052$ [+ GL] and 0.032 [– GL]).

Similarly, after controlling for latitudinal effects there were divergent responses for NSR and ISR to population density, with significant to marginally significant positive relationship of population density with ISR for several taxa, but not with NSR for any taxon. As a result, regressions with ISR had significantly higher slopes (NSR = 0.017 ± 0.017, ISR 0.09 ± 0.022, $P = 0.028$) and r^2 values (NSR = 0.026 ± 0.014, ISR = 0.089 ± 0.027, $P = 0.017$) than those with NSR (Table 2).

In contrast with the pattern seen for population density, both before and after correcting for latitudinal effects, NSR and ISR were both positively related to human population size (Table 2), with the latitude-corrected regression slopes (NSR = 0.13 ± 0.03, ISR = 0.15 ± 0.03, $P = 0.58$) and r^2 values (NSR = 0.12 ± 0.06, ISR = 0.12 ± 0.03, $P = 0.99$) not significantly different between the two groups.

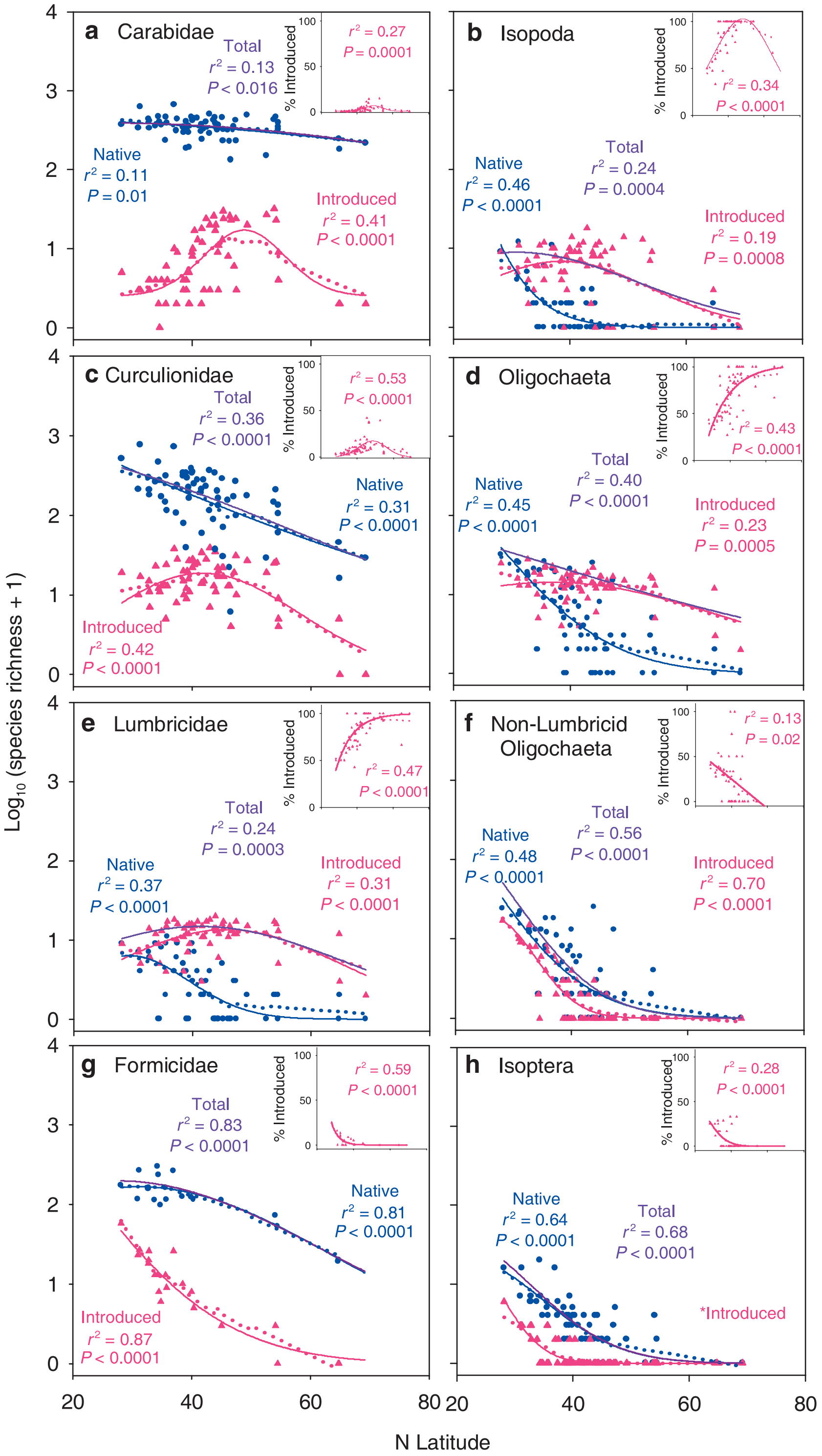

Figure 1 Relationship of latitude with native, introduced, and total species richness. Gaussian regressions of latitude against total, native, and introduced species richness in eight taxonomic groups. Points represent data for individual states or provinces of North America north of Mexico. Solid lines represent Gaussian fits. Dotted lines represent smoothed fits to the data (negative exponential fit, sampling proportion = 0.5, polynomial degree = 1). Insets represent the percentage of species that are introduced as a function of latitude, with *x* axis scale same as for main panel. Data points for total species richness were omitted for clarity. *Fit for log-introduced Isoptera failed to meet test assumptions of normality and constant variance but is presented for comparison of form of relationships for native and introduced species.

Summary of biogeographical patterns

In summary, for native species the dominant pattern was of negative relationships with latitude, positive relationships with human population size, and no relationship with distance from coasts or human population density (Table 4). Compared with native species richness, introduced species richness was more likely to have peaked relationships with latitude (for those taxa dominated by Palearctic species), similar relationships with human population size, more positive relationships with human population density, and more negative relationships with distance from coasts (Table 4). In general, for ISR relationships were strongest for latitude, intermediate for distance from coasts, and weakest for population density, with the most notable exceptions being Carabidae, which exhibited strong relationships with all four variables (Table 4).

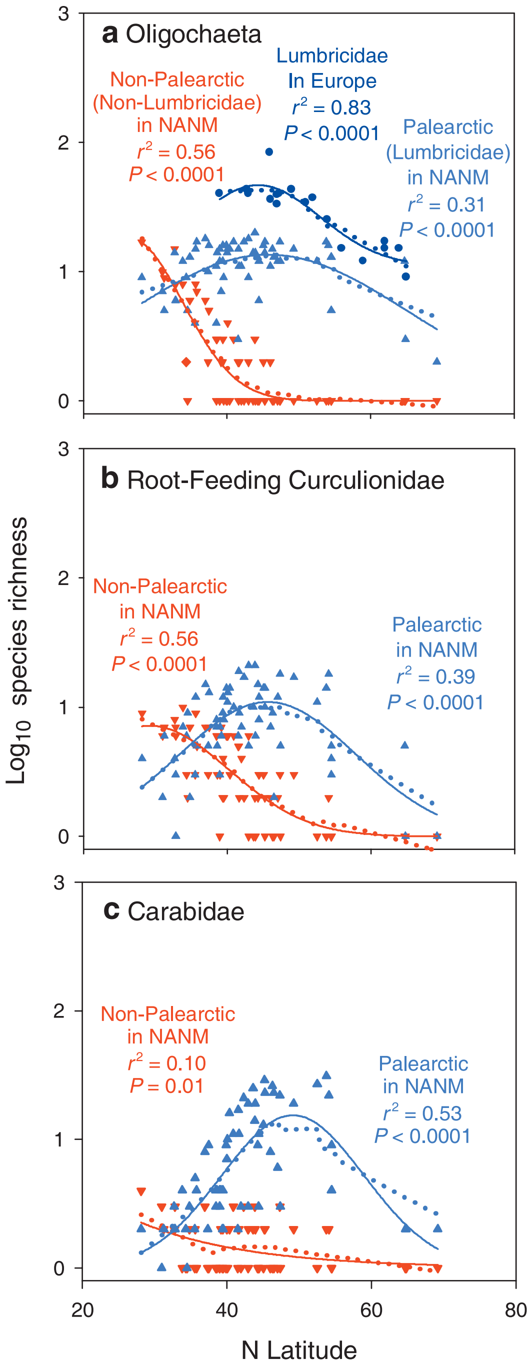

Figure 2 Effect of introduced species source region on latitude–richness relationships for three taxa of soil organisms. Solid lines represent nonlinear (Gaussian) regression fits (except for non-Palearctic Carabidae that were fitted with an exponential decay function because of the lack of convergence of the Gaussian function), dotted lines represent smoothed data (negative exponential, sampling proportion = 0.5, polynomial degree = 1) for comparison with the Gaussian regressions. Blue upward triangles represent richness of species with Palearctic origins, red downward triangles represent richness of species with non-Palearctic origins (a) Oligochaeta; dark blue circles represent Lumbricidae in Europe. (b) Root-feeding Curculionidae. (c) Carabidae.

Relationships of NSR and ISR

Relationships between ISR and NSR were positive for all taxonomic groups, but their strengths, slopes, and intercepts varied greatly (Fig. 3). All slopes were positive, and were significant ($P < 0.001$) for five taxa (Oligochaeta, non-lumbricid Oligochaeta, Formicidae, Isoptera, and Curculionidae) and non-significant ($P > 0.05$) for three (Lumbricidae, Isopoda and Carabidae) (Fig. 3). Intercepts were positive ($P < 0.0001$) for Isopoda, Oligochaeta, and lumbricid Oligochaeta, indicating that these introduced species occur consistently where natives are absent; non-significant ($P > 0.05$) for non-lumbricid Oligochaeta, Carabidae, and Curculionidae; and negative ($P = 0.02$) for Formicidae, indicating that natives occur where introduced species are absent. When the effects of latitude were statistically removed, NSR and ISR were positively related ($P < 0.05$) for all taxa tested (Table 3).

DISCUSSION

Richness–latitude relationships

This study demonstrates that human-accelerated novel species introductions have altered richness–latitude relationships for certain taxa (Oligochaeta, especially Lumbricidae; Isopoda). The convex ISR–latitude relationships exhibited by taxa dominated by species of Palearctic origin in NANM are strongly divergent from the monotonically declining total richness–latitude relationships typically found in other studies (Gaston, 2000; Willig *et al.*, 2003; Hillebrand, 2004) and exhibited by natives as well as introduced non-Palearctic (mostly subtropical and warm-temperate) taxa in the present study.

Northerly shifts in species richness for Lumbricidae and Isopoda in NANM have been significant enough that current total species richness–latitude relationships differ in form from pre-European NSR–latitude relationships, a striking human-induced perturbation of biogeographical patterns. These taxa appear to have been slow to recolonize northern regions since their elimination during the last glaciation (Jass & Klausmeier, 2000; Hendrix & Bohlen, 2002). Human introductions have led to a rapid acceleration of the colonization of the north by Palearctic taxa, with resultant reorganization of richness–latitude relationships. Whether the relative success of Palearctic taxa compared to Nearctic taxa in colonizing northerly latitudes is a result of the selection of Palearctic taxa by long association with human agriculture, escape of introduced species from biological control, or of other differences between Europe and North America in their glacial and faunal histories (Niemalä & Mattson, 1996), remains to be elucidated.

Sax & Gaines (2006) observed similar peaks in introduced species richness for several taxa, but did not explicitly compare native and introduced species richness. Furthermore, they used a different approach, summing richness over the entire latitudinal band rather than examining multiple smaller geographical regions. They discounted the significance of the observed peaks, hypothesizing that their results were an artefact of smaller land

Table 2 Effect of human population size and density on species richness for native and introduced species in eight taxonomic groups of macroinvertebrates. Results are slope, r^2, and P-values for the linear regression of the residuals of the richness–latitude regressions (from Fig. 1) versus $\log_{10}$ human population size and density for both native species richness (NSR) and introduced species richness (ISR).

	NSR–latitude residuals versus $\log_{10}$ population size			ISR–latitude residuals versus $\log_{10}$ population size			NSR–latitude residuals versus $\log_{10}$ population density			ISR–latitude residuals versus $\log_{10}$ population density		
Taxon	Slope	r^2	P	Slope	r^2	P	Slope	r^2	P	Slope	r^2	P
Oligochaeta	0.27	0.16	0.0008	0.15	0.18	0.0004	0.09	0.03	0.19	0.065	0.05	0.07
Lumbricidae	0.16	0.08	0.012	0.13	0.15	0.0013	0.067	0.03	0.21	0.067	0.06	0.05
Non-lumbricid Oligochaeta	0.24	0.15	0.0009	0.08	0.04	0.063	0.064	0.02	0.32	0.067	0.05	0.08
Isopoda	0.11	0.08	0.016	0.27	0.22	< 0.0001	0.020	0.004	0.61	0.07	0.02	0.23
Isoptera	0.14	0.14	0.0015	nd*	nd	nd	–0.02	0.005	0.58	0.037	0.08	0.03
Formicidae	0.04	0.00	0.41	0.12	0.16	0.038	–0.03	0.00	0.57	0.10	0.07	0.14
Carabidae	0.14	0.37	< 0.0001	0.20	0.13	0.0024	0.022	0.01	0.36	0.22	0.24	< 0.0001
Curculionidae	0.12	0.02	0.13	0.09	0.03	0.10	0.029	0.003	0.66	0.084	0.06	0.06

*Data for introduced Isoptera did not conform to the assumptions of least squares regression.

Table 3 Relationship of native and introduced species richness after removing the effect of latitude. The table 1ists the parameters for regression of log10 native species richness (NSR) versus $\log_{10}$ introduced species richness (ISR) after statistically correcting for the effects of latitude on species richness. Correction was achieved by using the residuals of species richness–latitude Gaussian regressions (from Fig. 1). Isoptera were not included because of deviations from assumption of constant variance in the initial regressions of ISR against latitude. N for non-lumbricid Oligochaeta and Isopoda was less than 62 because zero–zero comparisons were removed from the analyses.

Taxon	Slope	r^2	P	N
Oligochaeta	0.18	0.13	0.005	62
Lumbricidae	0.23	0.13	0.004	62
Non-lumbricid Oligochaeta	NA	0.31*	0.039	45
Isopoda	0.29	0.08	0.046	54
Formicidae	0.57	0.15	0.049	21
Carabidae	0.69	0.09	0.02	62
Curculionidae	0.45	0.39	< 0.0001	62

*Regression for non-Lumbricidae did not meet the assumptions of constant variance so Spearman's rho is presented instead of r^2.
NA, not applicable.

area at the lowest latitude in the temperate zone. Our results indicate that even when this possible artefact is removed by comparison of subregions, similar results are obtained. In addition, the divergent patterns we observed between native and introduced taxa indicate that factors other than land area are generating the patterns observed.

Studies of introduced and native plant diversity contain hints of similar mid-latitude peaks. In an analysis of introduced plants relationship with latitude that was approximately the inverse of ours, Lonsdale (1999) took the residuals of a multiple regression model of introduced species richness against a variety of factors (area, the residuals of an NSR–area regression, island–mainland status, reserve–non-reserve status) and regressed these residuals against latitude, finding a positive linear relationship between the two. This was interpreted as weakly supporting the hypothesis that temperate ecosystems are more invasible than tropical ecosystems. However, examination of these data (Lonsdale, 1999; fig. 8) indicates that the highest residuals were at mid-latitudes, between 30° and 40°, falling to negative at lower and higher latitudes. Thus, ISR richness–latitude relationships might have a mid-latitude peak in this data set as well. The data of Stohlgren *et al.* (2005) were also analysed using linear regression with the conclusion that latitude did not strongly predict either native or introduced species density. However, their data also exhibit what appears to be a mid-latitude (~40°) peak of richness, which in this case was evident for both native and introduced species. McKinney (2006) analysed for linear relationships of a variety of predictor variables, including latitude, with native and introduced species richness, but did not plot their data, so they cannot be examined for mid-latitude peaks.

We cannot definitively explain why the ISR–latitude relationships for Palearctic taxa are not monotonically declining in NANM. Current theory recognizes the disequilibrium nature of biogeographical patterns derived from processes of colonization, extinction, and speciation (Heaney, 2000). Of these three, colonization is most likely to drive short-term biogeography of introduced species.

Colonization can be divided into introduction, establishment, and spread. Geographical biases in any of these three processes could lead to the observed patterns. The long history of trade between northern Europe and North America favoured high rates of north-Eurasian species introduction. Climatic similarity between these regions would also favour establishment and spread. The patterns observed here are consistent with a model in which climate constrains the global diffusion of species in general (Turner, 2004) and introduced species in particular (Blackburn & Duncan, 2001). The expansive Palearctic land mass may

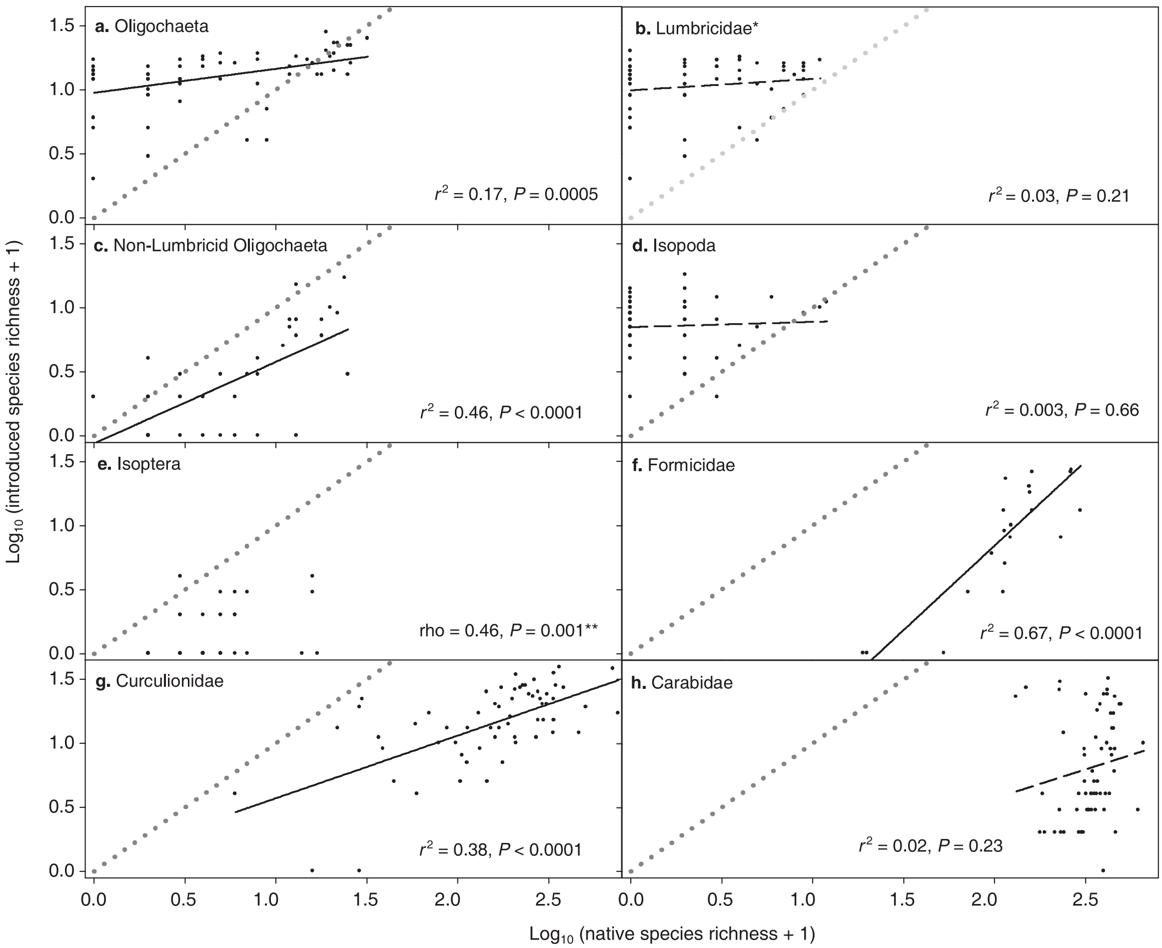

Figure 3 Relationship of native and introduced species richness. Least squares linear regressions of native versus introduced species richness ($\log_{10}$ transformed) for eight taxonomic groups of soil invertebrates. Significant regressions are represented by solid lines, non-significant regressions by dashed lines, 1 : 1 line by dotted lines. Each figure is labelled with the appropriate taxonomic group, r^2, and P-values for the regression. Sample points with zero–zero values were omitted from the analysis. N for each comparison: Oligochaeta = 62, Lumbricidae = 62, non-lumbricid Oligochaeta = 44, Isopoda = 53, Isoptera = 47, Formicidae = 21, Carabidae = 62, Curculionidae = 62. *r^2 and P-values are presented for untransformed data because transformed data violated assumptions of normality. **Linear fit from least squares regression did not meet assumptions of normality, so Spearman's rho and P-values are presented instead.

Table 4 Summary of relationships of native species richness and introduced species richness to latitude, distance from coasts, human population size, and human population density for several taxa of terrestrial macroinvertebrates.

	Native species richness				Introduced species richness			
Taxon	Latitude	Distance from coast	Population size	Population density	Latitude	Distance from coast	Population size	Population density
Oligochaeta	– ***	ns	+ ***	ns	P***	– ***	+ ***	(+)
Lumbricidae	– ***	ns	+ *	ns	P***	– **	+ **	(+)
Non-lumbricid Oligochaeta	– ***	ns	+ ***	ns	– ***	– *	(+)	(+)
Isopoda	– ***	(–)	+ *	ns	P***	ns	+ ***	ns
Isoptera	– ***	ns	+ **	ns	– ***	– *	nd	+ *
Formicidae	– ***	ns	ns	ns	– ***	ns	ns	ns
Carabidae	– *	ns	+ ***	ns	P***	– ***	+ **	+ ***
Curculionidae	– ***	ns	ns	ns	P***	– **	ns	(+)

–, +, and P represent negative, positive, and peaked relationships, respectively; ns (), *, **, and *** represent $P \geq 0.1$, < 0.1, < 0.05, < 0.01 and < 0.001, respectively.

have provided a large pool of potential invaders adapted to the temperate North American climate (Niemalä & Mattson, 1996).

Why these relationships are convex rather than some other shape, e.g. flat, is uncertain. One hypothesis is that the patterns are driven by climatic and/or biological gradients that are limiting at both lower and higher latitudes for these taxa. Alternatively, convex species richness–latitude relationships have been attributed to mid-domain effects, i.e. the overlapping of species' ranges at the centre of a shared and bounded geographical domain, thereby leading to a mid-domain peak of richness (Colwell & Lees, 2000). In NANM the southern boundaries are both hard (the Gulf of Mexico) and soft (the deserts of the south-western USA and northern Mexico). However, because most Palearctic species are adapted to mesic, temperate to boreal climates, the deserts may actually provide a relatively hard bioclimatic southern boundary for this group. Whatever the ultimate mechanisms, these data support a model of introduced species biogeography in which the dominant control on ISR–latitude relationships is the geographical (bioclimatic) origin of the introduced species.

Populated areas and coasts as hotspots of introduction or establishment

In the present study, both before and after correcting for latitudinal effects we found human population size associated with higher richness of both native and introduced species. This was also true for human population density before correcting for latitudinal effects. However, after correcting for latitudinal effects, population density was positively related only to ISR, not NSR. This indicates the need to account for two things in biogeographical analyses of introduced and native species: the different effects of population size and population density, and latitudinal effects on these patterns.

Human population size and population density are sometimes equated in discussions on population effects on species introduction. When study units are all of identical size, this equation is justified. However, when study units are of unequal size then the two are not equivalent. For example, in the present study log population size explained only a quarter of the variation in log population density ($r^2 = 0.25$, $P < 0.0001$). Studies in which area is not held constant have generally found, as in the present study, that there is a positive relationship between population size and both NSR and ISR (e.g. McKinney, 2006). These could be driven by area effects or by preferential selection of diverse regions for settlement by humans (Pautasso, 2007) combined with similar controls on both NSR and ISR (e.g. Gilbert & Lechowicz, 2005; Stohlgren *et al.*, 2005). Studies in which area is held constant have found positive relationships between plant and vertebrate species richness and human population density at the coarser spatial scales associated with the present study (Pautasso, 2007). Explanations invoked for the latter include the selection of diverse habitats for colonization by humans, or that humans have contributed to richness via species introduction (Pautasso, 2007).

Our finding that after correcting for latitudinal effects human population density was positively associated with ISR but *not* NSR is consistent with the hypothesis that high population density facilitates higher rates of introduced species establishment independent of the conditions that support native species richness. Possible drivers of this pattern are increased propagule pressure (Lockwood *et al.*, 2005; Colautti *et al.*, 2006; references therein), increased invasibility (e.g. Davis *et al.*, 2000), or both (e.g. Lonsdale, 1999; Rouget & Richardson, 2003). Our data cannot distinguish between these alternative drivers, but higher human population has been associated with higher levels of both propagule pressure and resource availability for invaders. Whatever the cause, our results support those of smaller-scale studies indicating that highly populated areas often have soil macroinvertebrate communities containing a high proportion of introduced species (e.g. Bolger *et al.*, 2000).

Interestingly, Pyšek *et al.* (2002), after correcting for effects of altitude (a bioclimatic analogue of latitude), found a positive effect of human population density on more recently arrived (neophyte) introduced species richness in nature reserves. Unfortunately, they did not examine whether human population density was positively associated with NSR.

Our finding of elevated ISR for some taxa near coasts suggests that these taxa have either higher rates of coastal introductions combined with slow rates of dispersal to interior sites, or higher probabilities of establishment in coastal regions because of more favourable abiotic or biotic conditions (Lindroth, 1957), or both. Coastal sites are commonly documented as points of introduction of invasive soil macroinvertebrates (e.g. Lindroth, 1957; Spence & Spence, 1988; Suarez *et al.*, 2001; Woodson *et al.*, 2001). The likelihood of higher propagule pressure near coasts is high because a diversity of vector pathways end or pass through ports in ships and their associated cargo, including soil ballast, horticultural material, and shipping containers. Use of soil ballast dumped on land from the 17th to early 20th century was likely a major mode of introduction for many of these species, because of the movement of large quantities of soil and the fact that unlike shipped goods, soil ballast was not moved beyond coasts (Lindroth, 1957; Kavanaugh & Erwin, 1985). As ballast was typically derived from coastal regions, many of the introduced ballast species are also likely to be well-adapted to coastal regions, favouring establishment in those regions and perhaps constraining spread away from coasts. In addition to ballast, introduction of soil macroinvertebrates in soil associated with horticultural or agricultural material was possible up until the second half of the 20th century (Spence & Spence, 1988). Although the banning of importation of soils has likely reduced the rate of influx of introduced soil organisms, certain species that are not obligate soil dwellers are still vectored by shipping (e.g. Tatem *et al.*, 2006) because high rates of species introduction are still associated with boats and ships, shipping containers, horticultural and agricultural material, military equipment, and other shipped goods (e.g. Robinson, 1999; Scheffrahn & Su, 2005; Suarez *et al.*, 2005).

There was some variation among taxa in the strength of their relationship with population density and distance from coasts. In particular, introduced Carabidae stood out as having especially strong relationships with both predictors. This corroborates the observations of Lindroth (1957) and Spence & Spence (1988) of strong association of introduced ground beetles with coastal areas and human disturbance. In contrast, ISR of non-lumbricid Oligochaeta exhibited relationships with coasts and human population that were no stronger than that of NSR. These divergences among taxa point to likely taxon-specific modes of introduction, establishment, or spread. However, our non-significant results for effects of population density and distance from coasts on ant species richness likely reflect the lower power of our analysis for ant trends because of the smaller samples for this taxon compared with the others, rather than a divergence of ant biogeographical patterns from those of other taxa.

Whether these patterns of elevated ISR near coasts and associated with high human population density will persist or dissipate over time depends on the ability of species to spread to interior areas, and those of lower population density. Analyses that take into consideration residence time and the environmental constraints on range size (Wilson *et al.*, 2007) should allow us to distinguish among these alternative models.

Relationship of native and introduces species richness

The positive relationship of NSR and ISR in the present study provides another line of support for the hypothesis that both native and introduced species richness respond similarly to environmental variables (e.g. Stohlgren *et al.*, 1999, 2005; Gilbert & Lechowicz, 2005). However, although all taxa exhibited positive relationships between native and introduced species richness, the relationship was very weak and non-significant for several taxa, whereas it was relatively strong for others. Some of this variation is likely due to the divergent relationships of NSR and ISR with environmental predictor variables, especially latitude. All three taxa with monotonic negative relationships between latitude and ISR (Formicidae, non-lumbricid Oligochaeta, and Isoptera) also had strong positive relationships between NSR and ISR. Of these three, the relationship for Isoptera was the weakest, probably because of the low diversity of introduced Isoptera. Of the four taxa in which ISR–latitude relationships diverged from NSR–latitude relationships, only Curculionidae had a significant relationship between NSR and ISR. For this taxon, ISR– and NSR–latitude relationships were relatively parallel for more than half of the latitudinal range examined, in contrast with Lumbricidae, Isopoda, and Carabidae. These patterns suggest that some of the variation in the relationship of ISR and NSR in the present study can be explained by the interaction of geographical origin of introduced species with latitudinal constraints, i.e. the introduction of Palearctic taxa has led to a weakening of positive NSR–ISR relationships. This is supported by the observation that after removal of latitudinal effects, most taxa exhibited positive relationships between NSR and ISR.

There was no evidence of biotic resistance, as none of the taxa exhibited negative relationships between ISR and NSR. However, this does not imply that biotic resistance is not functioning at some scales, but rather that there is no evidence of the predominance of biotic resistance over other processes at the large spatial scales examined in the present study.

Ecosystem effects and interactions with other stressors

Although introduced soil organisms affect ecosystems across the continent, mid-latitude highly populated coastal regions are likely to have the highest loading of unique suites of introduced soil organisms that can drive changes in soil processes (Oligochaeta and Isopoda), increase top-down effects on food-web structure (Carabidae), and increase rates of root and above-ground herbivory (Curculionidae). Functional consequences of these altered communities are only beginning to be appreciated, but could be substantial (e.g. Blossey & Hunt-Joshi, 2003; Bohlen *et al.*, 2004). The net impacts of these community changes will depend on the distribution, structure, and function of these newly assembled communities of native and introduced soil macroinvertebrates at landscape and finer spatial scales, e.g. on urban–rural gradients (e.g. Steinberg *et al.*, 1997) and from forest edge to interior (e.g. Bolger *et al.*, 2000).

In addition to introduced soil macroinvertebrates, these regions are subjected to a diversity of anthropogenic stresses such as other invasive species, landscape fragmentation, acid and nitrogen deposition, ozone exposure, and climate change. It is critical that we increase our understanding of how soil community reorganization will interact with these and other stress agents in influencing the structure and function of ecosystems.

CONCLUSIONS

To our knowledge, this is the first study to explicitly demonstrate divergent broad-scale biogeographical patterns for ISR and NSR relationships with latitude. It provides a statistical and conceptual model as a starting point for identifying the vulnerability of specific regions to invasion by different soil invertebrate taxa. We have begun to shed some light on the origin of these patterns, in particular the importance of source region in defining ISR–latitude relationships. This study is a model for a broader biogeographical approach to understanding the controls on introduced species richness that we hope will enhance both our understanding of the origins of global biodiversity and our ability to predict and prevent unwanted species introductions.

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