

the frequency band where natural flowers move. One reason moths might rely on both temporal and spatial adjustments to deal with low light (10) is to limit the costs to both motion-tracking performance and spatial resolution.

The frequencies with which a moth can maneuver could provide a selective pressure on the biomechanics of flowers to avoid producing floral movements faster than those that the moth can track in low light (22). The converse interaction—flower motions selecting on the moth—could also be important, suggesting a coevolutionary relationship between pollinator and plant that extends beyond color, odor, and spatial features (23) to include motion dynamics.

The emerging use of system identification to connect open- and closed-loop experiments (6, 14, 15, 18, 24, 25) provides a useful paradigm for exploring sensorimotor strategies in many systems. Robotic models enable rapid, repeatable experiments that extract critical features of the biological system (26) and extend the physical modeling toolkit that has been useful for teasing apart pollinator-plant interactions (7, 9, 23). Here the robotic flower enabled us to test predictions about closed-loop behavior from open-loop electrophysiological results and models of neural processing (6, 15).

The dual demands of acquiring reliable sensory information and maintaining motor performance are a general challenge, especially for animals such as *Manduca*, which operate in impoverished sensory environments (4–6, 27) and on the edge of flight instability (6, 25). Matching the requirements of the motor system to constraints imposed by the dynamics of the environment can provide strategies that enable more extreme sensory performance while averting tradeoffs in motor performance.

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BIOGEOGRAPHY

The dispersal of alien species redefines biogeography in the Anthropocene

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It has been argued that globalization in human-mediated dispersal of species breaks down biogeographic boundaries, yet empirical tests are still missing. We used data on native and alien ranges of terrestrial gastropods to analyze dissimilarities in species composition among 56 globally distributed regions. We found that native ranges confirm the traditional biogeographic realms, reflecting natural dispersal limitations. However, the distributions of gastropods after human transport are primarily explained by the prevailing climate and, to a smaller extent, by distance and trade relationships. Our findings show that human-mediated dispersal is causing a breakdown of biogeographic barriers, and that climate and to some extent socioeconomic relationships will define biogeography in an era of global change.

The reduced similarity in species composition between distant locations is one of the most noticeable patterns in nature (1–3). Dispersal limitation is at the heart of this pattern, either simply because of the accessibility of nearby locations or because environmental factors of ecophysiological importance tend to be spatially autocorrelated within the

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SUPPLEMENTARY MATERIALS

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range of natural dispersal (4). Notwithstanding, human trade and travel have been transgressing natural barriers to dispersal (5), and increasing numbers of species are becoming established in places far away from their native range (6, 7). Ultimately, this may cause the breakdown of the “classical” biogeographic regions (8)—mainly determined by dispersal barriers and historical factors such as continental drift or paleoclimates—and the emergence of new biogeographic arrangements determined primarily by environmental requirements and by geographic patterns in human transport pathways.

In recent centuries, and particularly during the past few decades, transport pathways have intensified in frequency and extended worldwide (5, 9). This accelerates the speed at which species colonize suitable areas across the globe and inherently contributes to the homogenization of species assemblages at a global scale (10–12). Niche theory and metacommunity theory suggest that the

breakdown of geographic dispersal barriers will allow species to progressively occupy their potential environmental niche (2, 13, 14), although other factors, such as the biotic composition of the receiving communities, may also play a role (15). This dispersal release should give rise to coherent spatial units reflecting environmental similarities among regions, and climatic similarities in particular (16, 17). Despite a strong theoretical rationale, clear evidence of a global, climate-filtered, biogeographic regionalization originated by human activity is still lacking.

Here, we report the results of a global-scale analysis comparing the biogeographic patterns of terrestrial alien gastropods before and after dispersal by humans. In contrast to most previous studies of biotic homogenization, our analysis is

global and therefore particularly appropriate to test the climate filter hypothesis. Regional studies capture only a fraction of worldwide climatic variation and are thus more likely to miss climatic signals. We also expect that increases in distributional equilibrium with climate should be particularly apparent for terrestrial gastropods because they are frequently introduced over long distances by means of trade (18, 19).

We collected national and subnational species lists of alien terrestrial gastropods, here defined as established alien species originating from human introductions after 1500 CE. We found data for regions across all continents except Antarctica, representing most of the major climatic types and biogeographic realms of the world (fig. S1 and table S1). For each alien species, we also identified

from the literature those regions in our data set that belong to their native range (fig. S2) (20). For simplicity, native range was defined as any location in which the species occurred before 1500 CE. This eventually may have led to the inclusion of a few locations to which the species were introduced earlier; however, those introductions have likely occurred within biogeographic realms (5, 9). Our alien distribution data set contained 802 occurrence records spread across 56 countries and subnational entities (e.g., federal states, islands), for a total of 175 species. The native distribution data set represented a subset of 140 species and 45 countries and subnational entities and contained 703 occurrence records.

We quantified pairwise compositional dissimilarity of the species lists in two ways: (i)

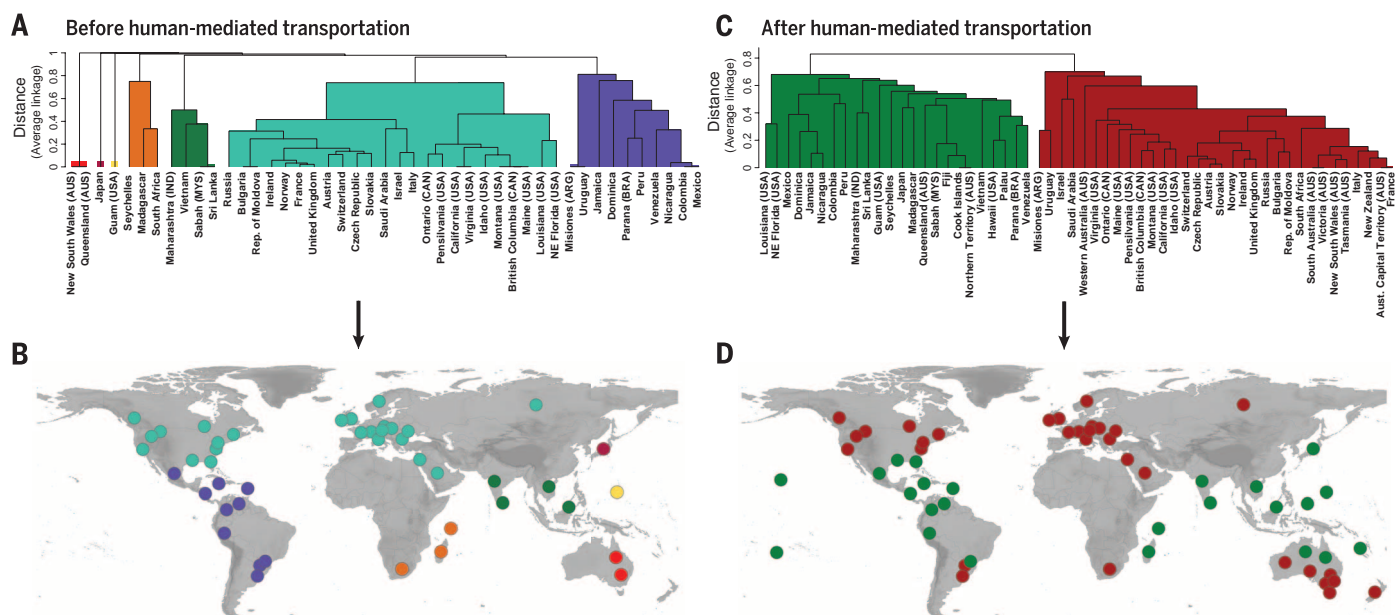
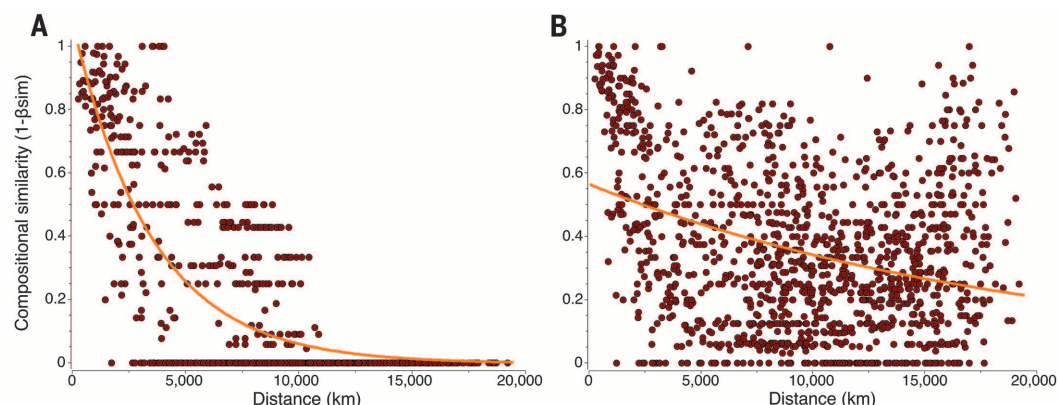


Fig. 1. Dendrogram and map of compositional similarities among lists of alien terrestrial gastropods. (A and B) Before dispersal by humans. (C and D) After dispersal by humans. Compositional dissimilarity of one location to the others [i.e., UPGMA (unweighted pair group method with arithmetic mean) grouping]. Colors indicate main clusters identified by the dendrogram and their corresponding locations in the world map.

Fig. 2. Relationship between compositional similarities of lists of alien terrestrial gastropods and geographical distances. (A) In native ranges. (B) In current ranges. Compositional similarities were measured by $1 - \beta_{sim}$. Relationship of compositional similarity for species in their native ranges was assessed on the basis of 990 unique pairs of 45 countries and subnational entities. Relationship for species in their current ranges is based on 1540 unique pairs of 56 countries and subnational entities. Model fits of exponential decay of compositional similarity with increasing distance are shown (orange). Model coefficients are provided in the text; tests of significance were obtained by comparison with distribution of coefficients generated from 1000 permutations of the matrix of compositional similarities.



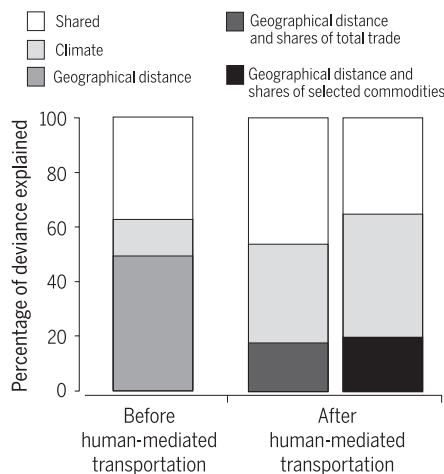


Fig. 3. Proportion of deviance explained in compositional dissimilarity of lists of alien terrestrial gastropods. Proportions are given for species in native ranges (i.e., before dispersal by humans; left bar) and for species in current ranges (i.e., after dispersal by humans; middle and right bars) and represent deviance that is explained by (i) climate- and dispersal-related predictors combined (white), (ii) climate alone (lighter gray), (iii) geographical distance alone (representing natural dispersal; mid-gray), and (iv) geographical distance and trade shares (representing anthropogenic dispersal) combined (darker gray and black). Climate is characterized by prevailing values of four variables: annual mean temperature, temperature seasonality, annual precipitation, and precipitation seasonality.

using only the native distribution, representing the spatial arrangement before human-mediated dispersal, and (ii) using both native and alien distribution, representing their current distribution. Dissimilarity was measured by the β_{sim} index (figs. S3 and S4). This is a standard metric in biogeographic studies (3, 27) because it accounts for differences in species richness. For each of the two dissimilarity matrices, we used an agglomerative hierarchical clustering algorithm (table S3) and nonmetric multidimensional scaling to analyze compositional dissimilarities among the lists (20).

Results from both analyses show that native-only distributions reflect “classical” broad-scale biogeographic patterns, which arose over geological time scales (Fig. 1A and fig. S5). For example, faunas located in the Australian, African, Oriental, Neotropical, and Holarctic biogeographic realms become clearly differentiated (Fig. 1, A and B) (1–3). Moreover, the compositional similarity (i.e., $1 - \beta_{sim}$) distinctly decreases with increasing geographical distance, indicating that dispersal limitations largely control these patterns (Fig. 2A, exponential decay rate of compositional similarity per 1000 km = -0.29 , $P < 0.001$). Highly similar species compositions ($1 - \beta_{sim} > 0.5$) do not occur at distances greater than ~6500 km, and none of the represented species are shared beyond ~11,000 km.

Combining the native and alien distributions of gastropods changes the grouping patterns: Species lists from temperate regions cluster into one group, while lists from tropical and subtropical regions cluster into another group (Fig. 1, C and D, and fig. S6). For example, regions in temperate North America (e.g., Virginia, California, British Columbia) have, on average, a higher proportion of species shared with sites in other temperate but distant regions of the world, such as Europe, New Zealand, southern Australia, or South Africa, than with “nearby” (sub)tropical regions such as Florida, Louisiana, México, or Jamaica. This bipartite division of species compositions into two latitudinal biogeographic regions—a (sub)tropical belt and a region composed by temperate to arctic areas in both hemispheres (Fig. 1D) (2)—suggests a reorganization of species distributions constrained only by climate. Within each of these broad regions, compositional differences and geographical proximity remain associated (see subclusters in Fig. 1C); however, at the global scale, the arrival of aliens leads to the weakening of the distance decay of similarity (Fig. 2B, exponential decay rate of compositional similarity per 1000 km = -0.05 , $P < 0.001$) and to the occurrence of highly similar species compositions ($1 - \beta_{sim} > 0.5$) along the whole range of geographical distances (i.e., up to ~19,000 km).

To explicitly test for the role of climate in shaping biogeographic changes, we tested climate as a predictor for compositional dissimilarity before and after human-mediated dispersal. For species in native ranges (i.e., before human transportation), we compared the explanatory power of climate (as represented by prevailing values of annual means and seasonality of temperature and precipitation) (20) with that of geographical distances (which we assume to represent dispersal limitations) (4). For the analysis of combined native and alien distributions (i.e., after human dispersal), we additionally accounted for the role of anthropogenic dispersal. Because global patterns of introduction of terrestrial gastropods are primarily determined by commodity trading (18, 19), we used bilateral trade shares as proxy. We calculated this variable in two alternative ways: (i) considering all traded commodities (a general indicator of trade integration among the countries), and (ii) considering only those commodities that are known vectors of gastropods (e.g., household tiles, live plants, or fresh vegetables and fruits for consumption) (18, 20). Because bilateral trade data are not available for most subnational entities, the tests were performed using country-level data representative of the biogeographic groupings identified above (figs. S7 to S12) (20).

Monte Carlo permutation of generalized dissimilarity models (22) shows that climate and geographical distance are both significant predictors of native-range compositional dissimilarities ($P < 0.001$) (20), accounting together for about 61% of total deviance. However, the partitioning into unique and shared components of the factors (20) reveals that the unique explan-

atory power of geographical distance (representing dispersal limitation) is much greater (proportion of total explained deviance = 49.5%) than that of climate (proportion of total explained deviance = 13.3%) (Fig. 3). In contrast, for the current distribution of gastropods (i.e., including both native and alien ranges), climate rather than dispersal becomes the most important predictor. More specifically, when used jointly, both climate- and dispersal-related variables (i.e., geographical distances and trade shares) are significant predictors of current patterns of compositional dissimilarity ($P < 0.001$), accounting for about 63% of its total deviance. But the unique contribution of climate to the total explained is now about 2 to 2.3 times that of the unique contribution of dispersal (climate = 36.4% and dispersal represented by geographical distance and shares of selected commodities = 19.6%) (Fig. 3). We cannot exclude the possibility that anthropogenic dispersal pathways that covary with climate (23) may also have contributed to the formation of this pattern; however, the reduced relative influence of dispersal-related variables in explaining current distribution patterns suggests that this process, if causative, is of moderate importance.

Signs of ongoing and intensifying biodiversity change are increasingly ubiquitous (24, 25). Still, a recent global analysis of monitoring studies found no significant changes in local species richness, but instead a strong temporal species turnover (6). Human-mediated dispersal of species has already caused substantial biotic intermixing worldwide (12, 26, 27) and may contribute to this turnover. Biotic intermixing is predicted to continue or even intensify in the future (5, 28). The resulting “biogeography of the Anthropocene” defies physical boundaries and reduces compositional dissimilarities among distant regions (7). However, our results suggest that instead of a progression toward a uniform biosphere, ecophysiological limitations will cause a higher prevalence of biotic homogenization among areas sharing similar environments. Our results also suggest that homogenization will be greater among regions that have intense trade relations and that are closely located. These novel species assemblages will be dominated by relatively few but widespread alien species, which mostly consist of competitive generalists (10). This profound biogeographic reorganization will put additional pressure on native biota [e.g., (29)]. A recent international assessment has shown that the rate of alien introduction events shows no signs of abating (30). Renewed efforts are needed to slow biotic homogenization if the targets of the Convention on Biological Diversity for 2020 are to be met (30).

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SUPPLEMENTARY MATERIALS

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INNATE IMMUNITY

Cytosolic detection of the bacterial metabolite HBP activates TIFA-dependent innate immunity

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Host recognition of pathogen-associated molecular patterns (PAMPs) initiates an innate immune response that is critical for pathogen elimination and engagement of adaptive immunity. Here we show that mammalian cells can detect and respond to the bacterial-derived monosaccharide heptose-1,7-bisphosphate (HBP). A metabolic intermediate in lipopolysaccharide biosynthesis, HBP is highly conserved in Gram-negative bacteria, yet absent from eukaryotic cells. Detection of HBP within the host cytosol activated the nuclear factor κ B pathway in vitro and induced innate and adaptive immune responses in vivo. Moreover, we used a genome-wide RNA interference screen to uncover an innate immune signaling axis, mediated by phosphorylation-dependent oligomerization of the TRAF-interacting protein with forkhead-associated domain (TIFA) that is triggered by HBP. Thus, HBP is a PAMP that activates TIFA-dependent immunity to Gram-negative bacteria.

The mammalian innate immune system detects microbes by recognizing pathogen-associated molecular patterns (PAMPs) that are absent from the host yet broadly conserved among classes of microbes (1, 2). However, in many cases, the specific microbial patterns responsible for inducing protective immunity are unclear, suggesting that additional PAMPs may exist that alert the immune system to the nature of a pathogen.

The human pathogens *Neisseria meningitidis* and *Neisseria gonorrhoeae* release a heat-resistant molecule that activates the transcription factor nuclear factor κ B (NF- κ B) in human embryonic kidney (HEK) 293T and Jurkat T cells—cell types whose ability to respond to PAMPs was thought limited to detection of flagellin by Toll-like receptor 5 (TLR5) (3). We previously showed that the *Neisseria* gene *hldA* was required for this molecule's production (3). HldA catalyzes the second step in the adenosine 5'-diphosphate (ADP)-heptose biosynthetic pathway, which supplies the precursor for heptose residues found within the inner core of lipopolysaccharide (LPS) (fig. S1A). We tentatively identified a heptose-containing metabolite downstream of HldA as the activating molecule (3), yet the specific identity of the active conformation remained unknown. Therefore, we took a genetic approach and examined the ability of culture supernatants from bacterial mutants of the ADP-heptose pathway to activate NF- κ B. Although HldA was essential, the ensuing enzymes in the pathway were not (Fig. 1A), indicating that the product of HldA, D-glycero-D-manno-heptose-1,7-bisphosphate (HBP), was both necessary and sufficient for NF- κ B

activation. Both Δ *gmhB* and Δ *hldA* *N. meningitidis* display the “deep-rough” phenotype (4), possessing a truncated, heptose-less lipooligosaccharide (LOS) (Fig. 1B), which indicates that the proinflammatory ability of HBP is independent of the incorporation of heptose into the LOS. To confirm this notion, we enzymatically synthesized and purified HBP from sedoheptulose-7-phosphate, using recombinant GmhA and HldA. The reaction product potentially stimulated NF- κ B only when the substrate and both enzymes were supplied (Fig. 1C), and the activity decreased when the downstream phosphatase GmhB was added (Fig. 1D). Finally, we performed mass spectrometry to show that the proinflammatory product of the GmhA-HldA reaction was indeed HBP (fig. S1, B and C). Thus, HBP is the innate immune agonist shed by *Neisseria*.

Transcriptome analysis identified primarily NF- κ B target genes as induced by HBP in Jurkat cells (fig. S2A). The kinetics of HBP-induced transcription and NF- κ B activation was slower than stimulation with flagellin or tumor necrosis factor- α (TNF α), both of which signal extracellularly (fig. S2, B to D). Therefore, we considered whether HBP required entry into the host cytosol to signal. Indeed, using reversible digitonin permeabilization (5) to deliver HBP-containing supernatants into the cytosol of Jurkat IG5 cells, which harbor an NF- κ B-dependent HIV long terminal repeat (LTR)-luciferase construct (6), increased luciferase activity, whereas TLR5 activation was unaffected (Fig. 1E). Moreover, an inhibitor of the guanosine triphosphatase dynamin (7) attenuated the NF- κ B response to HBP (fig. S3A), indicating that HBP can enter cells via dynamin-dependent endocytosis. HBP enhanced signaling by TLR ligands in THP-1 macrophages, yet did not induce inflammatory cell death (fig. S3, B to D). Finally, HBP induced proinflammatory cytokine production from primary human immune and nonimmune cells (fig. S4, A to C).

The ADP-heptose biosynthetic pathway is highly conserved among Gram-negative bacteria (8)

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Supplementary Materials for

The dispersal of alien species redefines biogeography in the Anthropocene

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Materials and Methods

Distributional data collection and pre-processing

We gathered all national or subnational lists we could find of alien terrestrial gastropods (i.e. land snails and slugs) across the world. Searches were made in electronic documents, scientific literature and technical reports. All data were checked in order to ensure geographical, temporal and taxonomic consistency. Accordingly, we excluded outdated lists (i.e. older than 15 years, with 2014 as reference year) and lists for which we could not assign a precise geographical delimitation. Incomplete lists which ignored some species groups were also excluded, except when full taxonomic coverage was obtained through the combination with other sources. In total, we used 54 data sources (complete list in table S1), describing the pool of alien terrestrial gastropods for 35 national and 24 sub-national entities across the world (fig. S1).

Next, we “cleaned” and standardized the distribution data provided by each list. First, we converted all infraspecific statuses into single species occurrences and removed any records referring only to higher taxonomic levels. We also removed all records for which a species’ establishment or nativity status was mentioned as uncertain or for which establishment was only known in closed man-made environments (e.g. greenhouses). As our aim was strictly biogeographical – i.e. pertaining to species distributions –, we made no distinction of species based on the impacts they caused in the alien range, i.e. if the species were invasive *sensu* (31) or not. We checked species names for synonyms. We used the National Center for Biotechnology Information (NCBI) taxonomy database (32) and further relevant literature (33–38) to identify redundancies among species designations. Given the absence of a widely accepted global checklist for gastropods (33), we accepted the most commonly used species name in the lists. To reduce taxonomic uncertainty in the records of several *Arion* slugs that form cryptic species complexes (39), we grouped these species according to their broad sense designation. Accordingly, the *Arion ater* group included *A. ater*, *A. rufus* and *A. vulgaris*; the *Arion fasciatus* group included *A. silvaticus*, *A. circumscriptus* and *A. fasciatus*; the *Arion hortensis* group included *A. hortensis*, *A. owenii* and *A. distinctus*; and the *Arion subfuscus* group included *A. subfuscus* and *A. fuscus* (40). Altogether, our alien distribution data set provided information on 175 species. To our knowledge this is the by far most complete, up to date, database on the alien distribution of terrestrial gastropods worldwide.

For each alien species, we also identified those regions in our data set that belong to their native range. The use of the same set of species and of regions ensures the comparability of detected patterns. For most regions the assessment of nativity status was based directly on the lists reporting alien species – as many of these also listed native species. For the remaining areas (Argentina; Austria; Czech Republic; Fiji; Hawaii; Israel; Japan; Madagascar; New Zealand; Norway; Slovakia; South Africa; Sri Lanka; Switzerland; Venezuela) we used newly collected native-only species lists and relevant literature (33, 34, 37, 41–54). Because some species were not native in any of the areas surveyed and some areas were not within the native range of any species, the native distribution data set

comprised a subset of all species and areas found in the alien distribution data set. In total, the native distribution data set encompassed 35 national and 17 sub-national entities (fig. S2).

Identification of spatial patterns of compositional differences

We performed cluster and ordination analyses of compositional dissimilarity based on species lists formed by i) the species native distributions (i.e. aliens on their native ranges) and by ii) their current distributions (i.e. aliens on their native and alien ranges). In both cases, we used the distribution data that was collected for national and subnational entities. When spatial overlap occurred among these entities, we retained only the one providing higher spatial resolution (e.g. a federal state within a country). After this procedure, the native distribution data set was represented by 28 countries and 17 sub-national entities and the alien distribution data set by 32 countries and 24 sub-national entities. We computed pairwise matrices of compositional dissimilarity among areas using the β_{sim} index (55, 56). This metric is particularly suited for biogeographic studies because it is robust to differences in species richness and thus reduces confounding effects that may originate from variation in species-area relationships, colonization pressure or sampling efforts (3, 21). This index is calculated as $1 - [a / (\min(b, c) + a)]$, where a is the number of species shared by the two location, b is the number of species unique to the first location, and c is the number of species unique to the second location. The β_{sim} index ranges from 0 to 1, with 0 indicating complete similarity and 1 complete dissimilarity (see results in figs. S3 and S4).

Before proceeding with cluster and ordination analyses we tested the sensitivity of the values of compositional dissimilarity to potential errors in the data as caused, for example, by taxonomic misidentifications, incorrect assignments of nativity status or unidentified synonyms in species designations. To simulate the effect of errors, we randomly permuted species and regions records. Full permutation of records was performed for individual species and regions and for random selections of 5, 10, and 15% of all species and of all regions. We measured the relative influence of these artificial errors on the calculation of compositional dissimilarities by calculating the correlation (using a Mantel test) between the resulting dissimilarity values with the dissimilarity values found in the corresponding original data set. To allow for variation in the random permutations, we repeated the previous process 100 times for each simulated data set. We found that the permutation of records for a single species had a negligible effect in the calculation of compositional dissimilarities, with reductions in correlation with original values being lower than 0.01 for all datasets (table S2). Permutation of records for individual regions were more influential, but nevertheless all correlations with original values of compositional similarity remained very high ($r > 0.95$). Increases in the number of species or regions randomized reduced the correlation values. Nevertheless, simulating that 10% of all species or regions corresponded to spurious records (e.g. unresolved synonymies) still renders a high correlation with original dissimilarity values ($0.96 > r > 0.81$). These results suggest an overall robustness of the calculation of dissimilarity values to potential errors in species or region records.

We analyzed the similarity of species compositions using three clustering techniques commonly used in biogeographical studies (3, 21, 57): unweighted pair-group method using arithmetic averages (average linkage; UPGMA); weighted pair-group method using

arithmetic averages (McQuitty's method); weighted pair-group method using Ward's method (minimum variance). We also analyzed the data using nonmetric multidimensional scaling (NMDS). These calculations were performed in R ver. 3.0.2 (58). NMDS was fit using the package *smacof* (59) using a convergence limit of 1×10^{-5} and a maximum of 2000 iterations.

Descriptive accuracy of hierarchical clusters was evaluated with the cophenetic correlation coefficient, which measures the extent to which clusters (in the form of a cophenetic matrix) correspond to the original compositional dissimilarity matrix (60). This coefficient showed that UPGMA provided the most accurate hierarchical representation of pairwise dissimilarities (i.e. closer to a correlation value of 1) for both native and current ranges ($r = 0.91$ and $r = 0.82$, respectively). Given the lower accuracy of the other hierarchical approaches (table S3), we did not consider their results any further.

The reliability of NMDS projections in a two-dimensional space was assessed by the stress value, which measures the agreement between quadratic sums of original distances and distances in the NMDS ordination space (60). In both cases (i.e. for native distributions and for current distributions) the value of this metric was extremely low (4.1×10^{-5} and 0.03, respectively) supporting a high reliability of the two-dimensional projections.

Importantly, the results of UPGMA and NMDS were congruent. For native ranges, both methods showed the separation of Japan, Guam and New South Wales and Queensland (the only two Australian subnational entities included in this analysis) (Fig. 1AB and fig. S5). The remaining areas appear more closely grouped, but the differentiation of African, Holarctic, Neotropical and Oriental realms remains clear in the results of both methods (Fig. 1AB and fig. S5). For current distributions, the emergence of two large groups differentiating (sub)tropical from temperate regions (see main text) is also supported by both UPGMA clusters and NMDS ordination. In UPGMA this is given by the first split in the dendrogram (at $\beta_{\text{sim}} = 0.83$), which distances about 0.15 to the average of dissimilarity among (sub)tropical areas ($\beta_{\text{sim}} = 0.68$) and 0.13 to the average of dissimilarity among temperate areas ($\beta_{\text{sim}} = 0.7$) (Fig. 1C). In the NMDS ordination plot, this division is displayed by the grouping of (sub)tropical regions on the right side of the plot and of temperate regions on the left side (fig. S6).

Patterns of compositional dissimilarity for country-only data

Because trade-share data are only available at the country level, we tested the relative role of dispersal and climate as predictors of patterns of compositional dissimilarity using country-level data only (see main text). Therefore, we evaluated if the statistical grouping of compositional dissimilarities across countries was congruent with the patterns observed for countries and subnational entities combined (see above). Our native only distribution data set encompassed 30 countries (i.e. all that were within the native range of any species being alien in the other countries) and the data set of current distributions encompassed 35 (fig. S1). For each of these two data sets we calculated pairwise matrices of compositional dissimilarity (using β_{sim}) and evaluated overall resemblance in species compositions using the same four

statistical techniques used in the analysis of data for countries and subnational entities combined (i.e. UPGMA; McQuitty; Ward and NMDS, see above). Similarly to the results obtained for countries and subnational entities, the hierarchical description of country-level data was best described by UPGMA (cophenetic correlation: 0.95 for native ranges and 0.85 for current ranges) (table S3), and the two-dimensional ordinations of NMDS were also highly reliable (stress = 4.6×10^{-5} for native ranges; stress = 0.02 for current ranges).

Grouping patterns for country-level data strongly resembled the patterns found for countries and subnational entities combined. Native distributions reflected “classical” biogeographical patterns, with countries belonging to the same biogeographical realm being consistently close to one another (figs. S7 and S8). Likewise, species’ current distributions at the country-level highlighted the same (sub)tropical/temperate division found for countries and subnational entities combined (figs. S9 and S10).

The distance-decay relationships of country-level data also matched those of countries and subnational entities combined. For native distributions, both datasets show a strong decline in compositional similarities as geographical distances increase (exponential decay rate of compositional similarity per 1000 km for countries and subnational entities and for countries only = -0.29, $P < 0.001$), highly similar compositions ($\beta_{\text{sim}} < 0.5$) are restricted to distances smaller than ~6,500 km and there are no shared species beyond ~11,000 km (Fig. 2A and fig. S11).

Likewise, the two data sets show the same marked weakening of the distance decay of similarity when alien distributions are combined with native ranges (exponential decay rate of compositional similarity per 1000 km for countries and subnational entities = -0.05, for countries only = -0.09, $P < 0.001$), and the occurrence of highly similar compositions ($\beta_{\text{sim}} < 0.5$) along the whole range of geographical distances examined (Fig. 2B and fig. S12).

Testing dispersal and climate as predictors of compositional dissimilarity

Commodity trade data

Humans have deliberately introduced terrestrial gastropods in new areas for several reasons (e.g. usage as ornamentals, food resource or biocontrol agents), however, the large majority of introductions has been inadvertent and is related to the movement of human commodities (18, 19). Using data from interceptions in cargo arriving in the USA, Robinson (18) analysed the main vectors of terrestrial gastropods, and found that, altogether, house-hold tiles, cut flowers, horticultural plants, fresh fruit, vegetables and herbs as well as the containers carrying these and other commodities accounted for about 75% of all interceptions. Apart from personal baggage (3.7%) and military cargo (1.2%), the remaining vectors represented each less than 1% of total interceptions made. Based on these findings we used commodity trade data to represent patterns of anthropogenic dispersal of terrestrial gastropods. We used data from the United Nations commodity trade statistics database (UN Comtrade) (61) which provides values of bilateral trade (in US dollars) between countries at the commodity level starting from 1962. For each country composing the dataset of species current distributions ($n = 35$), we calculated the percentage of trade (i.e. trade share) with each of the other countries.

This was calculated as the value of total trade (imports and exports) of country i with country j divided by the value of total trade of country i with the world (62). We performed these calculations in two alternative ways, a first considering only the main vector commodities identified by (18) (harmonized system codes: 06; 07; 08; 680221; 680222; 680223; 680229; 690490; 690510; 6907; 6908) and a second considering all traded commodities. In both cases, a high share indicates a high importance of country j in the total flow of commodities exchanged by country i .

Climatic data

We described global climatic gradients using four climatic variables, mean annual temperature; mean annual precipitation; temperature seasonality and precipitation seasonality. These variables were taken from the WorldClim database (63) at 10 arc-min pixel resolution and are based on meteorological data recorded from 1950 to 2000. We averaged these variables over each country in our database and used pairwise Spearman rank correlations to confirm their non-redundancy (i.e. $|\rho| < 0.75$). The choice for these variables reflects the high importance of temperature and humidity on the physiology of terrestrial gastropods (64, 65).

Explanatory power of climate before and after human-mediated dispersal

As an initial test of the importance of climate in determining patterns of compositional dissimilarity, we performed a univariate exponential decay fit between climatic conditions and pairwise compositional dissimilarities for species in 1) their native ranges and in 2) their current ranges. The climatic predictor corresponded to Euclidean distances on scaled values (from 0 to 1) of mean annual temperatures and total annual precipitation for each pair of sites. We found that climate was a much better predictor of compositional dissimilarities for species in their current ranges than in native ranges (pseudo R^2 for native distributions = 0.16; pseudo R^2 for current distributions = 0.36; fig. S13).

Comparing the explanatory power of dispersal and climate

We used generalized dissimilarity modelling (GDM) (22) to compare the contribution of dispersal and climate in explaining spatial patterns of compositional dissimilarity. GDM is an I-spline-based extension of matrix regression that accounts for nonlinearities between explanatory variables and compositional dissimilarities. Unlike classical linear matrix regression, GDM is capable of i) fitting variation in rates of compositional dissimilarity along the gradient of each environmental variable (i.e. non-stationarity), and of ii) fitting curvilinear relationships imposed by the use of a dependent variable that is constrained to a 0-1 interval (i.e. dissimilarity cannot extend beyond 1, even if environmental differences continue to increase) (22). This flexibility of GDM is important in the analysis of our data, which spans wide (global-scale) environmental gradients – and for which substantial deviations from stationary conditions are likely (22) –, and also because native distributions have a high

proportion of site pairs that have no species in common (i.e. $\beta_{\text{sim}} = 1$) (Fig. 2A). Here the flexibility of GDM was constrained to the default of three I-spline basis functions per predictor.

We analysed compositional dissimilarities for species in native and in current ranges using matrices calculated for country-level data. GDM models for species in native ranges used climatic variables and geographical distance as predictors. Geographical distance was measured from country centroids, and was used as a proxy for natural dispersal limitations (4, 22, 66, 67). For species in current ranges (i.e. after the transportation of species by humans) we added trade-shares as a predictor. Because each pair of countries (i, j) is characterized by two trade-share values (T_{ij} / T_i and T_{ji} / T_j), we selected the one in which the country used as denominator was the same that was used as denominator in the calculation of β_{sim} – i.e. the total of trade and the total of species used in each of the calculations belonged to the same country. The assumption tested is that the higher the importance of a country in the total trade of another, the more species of the later will be shared with its partner. Because GDM assumes that higher pairwise difference in the values of the predictors corresponds to a higher dissimilarity between sites (i.e. to a lower relatedness) (22), we inverted the values of trade-shares by subtracting them from 1. We tested two alternative GDM models for current distributions, one using traded-shares of selected commodities, and the other using traded-shares of all commodities. In both cases the predictors were log-transformed.

We also accounted for the effect of country size in the representativeness of centroid-based distances and average climatic conditions. For this purpose we ordered countries by decreasing sizes and set the weight of each observation in the model to be equal to order position of the wider of the two countries in the pairwise comparison. These ranked weights were preferred over area-proportional weights because the later would imply an overweighing of a few small island countries (e.g. Cook Islands, Palau or Seychelles). Models using weighted observations provided results that are qualitatively similar to those using equal weights (Fig. 3 and fig. S14). However, the latter models always explained a higher deviance in compositional dissimilarities (main text and fig. S14) and we only refer to them in the main manuscript.

To test for the significance of the predictors, we subjected all models to a backward variable selection procedure based on Monte Carlo permutation tests. We first fitted the GDM model using all predictors. Next, we measured the reduction in explained deviance caused by the removal of the least informative predictor. If the reduction in explained deviance caused by the removal of the predictor was lower or equal than the explained deviance verified in equivalent models using a randomly permuted response variable, the predictor was considered non-significant and removed from the model (66 – 68). Based on differences of deviance between 1000 permuted models, predictors representing climate and dispersal had significant unique contributions in all models ($P < 0.001$).

We measured the relative importance of dispersal and climate in explaining patterns of compositional dissimilarity by partitioning their unique and shared contribution to the total of deviance explained (D) by the GDM models (65, 67). To perform this, we fitted compositional dissimilarities using i) only dispersal related predictors (GDM_{dis}) (i.e. geographical distances for native distributions and geographical distances in combination

with one of the trade-share variables for current distributions), ii) only climatic predictors (GDM_{clim}) and iii) all predictors simultaneously (GDM_{all}). The unique contribution of dispersal (I_{dis}) was calculated as $D(GDM_{\text{all}}) - D(GDM_{\text{clim}})$; the unique contribution of climate (I_{clim}) as $D(GDM_{\text{all}}) - D(GDM_{\text{dis}})$, and the shared contribution of the two predictor types as $D(GDM_{\text{all}}) - (I_{\text{dis}}) - (I_{\text{clim}})$. Results were converted to percentages where $D(GDM_{\text{all}}) = 100\%$.



Fig. S1. Countries and sub-national entities covered by the alien distribution data set. Note that in order to avoid pseudo-replication of data, the national lists of Argentina, Australia and Canada were not included in analyses combining national and subnational entities because they nested available subnational lists. These lists were considered for country-level analyses only.



Fig. S2. Countries and sub-national entities covered by the native distribution data set. Note that in order to avoid pseudo-replication of data, the national lists of Argentina, Australia and Canada were not included in analyses combining national and subnational entities because they nested available subnational lists. These lists were considered for country-level analyses only.

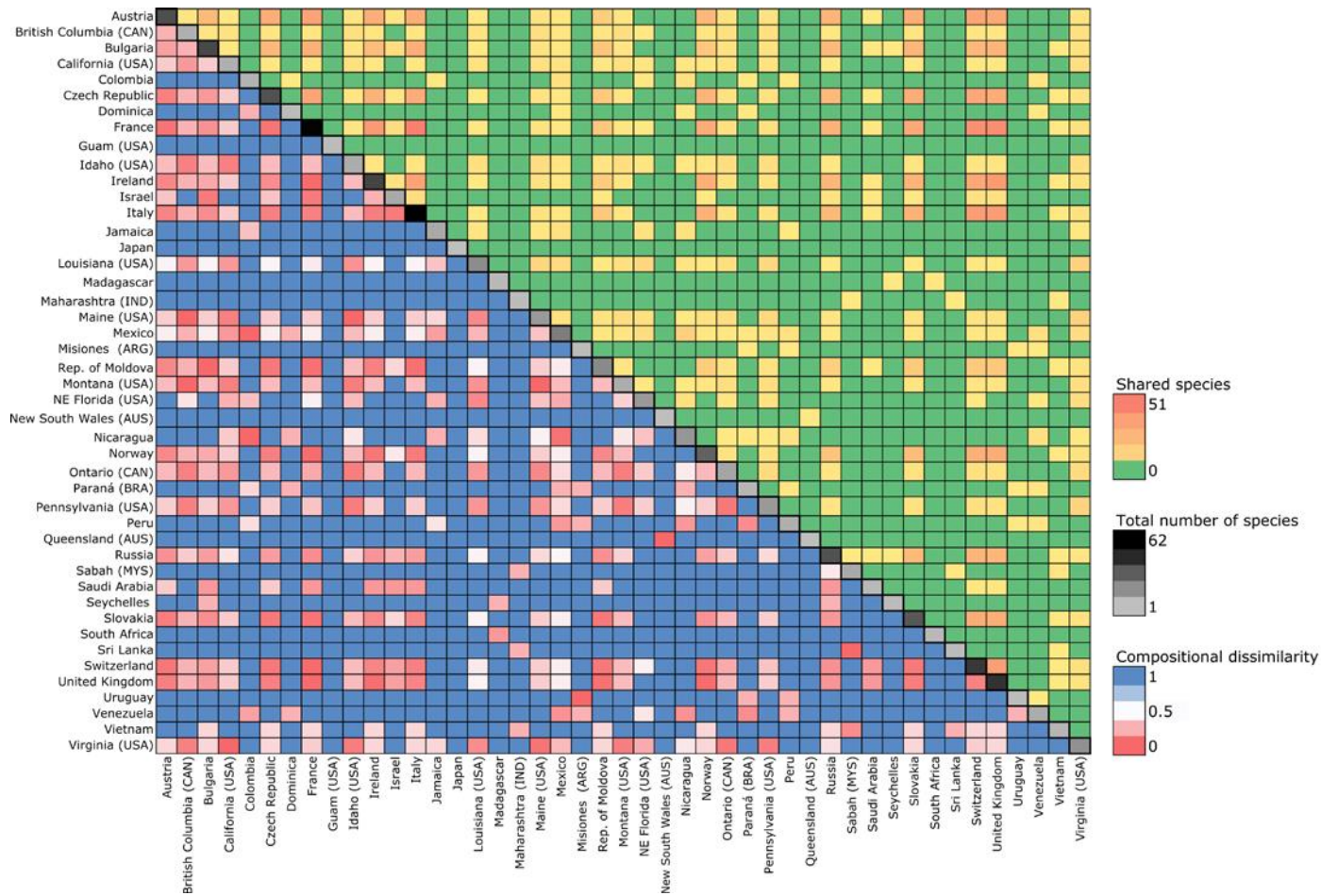


Fig. S3. Pairwise compositional dissimilarities for species in their native ranges. The lower triangle shows the values of compositional dissimilarity, the upper triangle shows the total number of species that are shared between each pair of areas and the main diagonal shows the total number of species of each area.

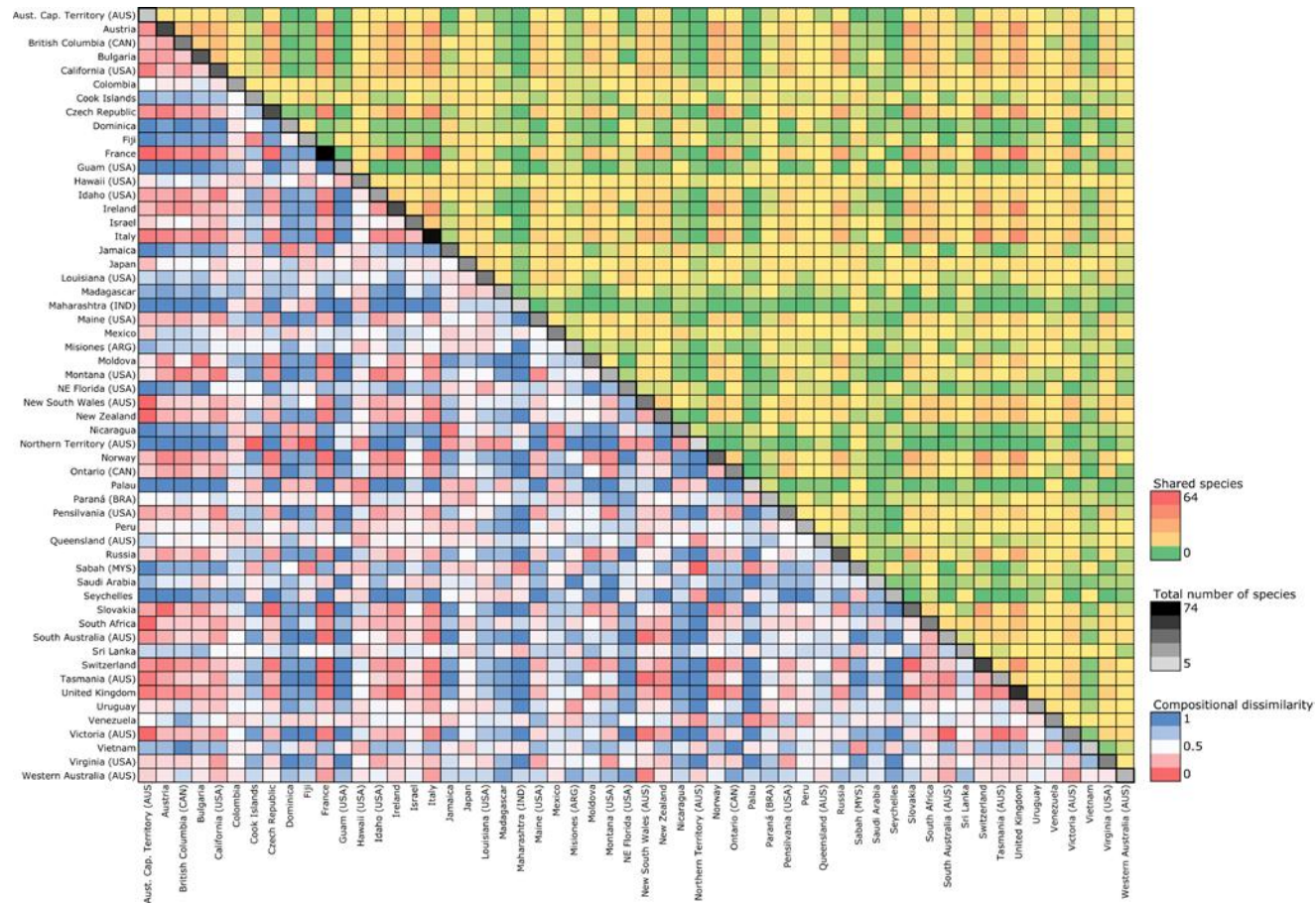


Fig. S4. Pairwise compositional dissimilarities for species in their current ranges. The lower triangle shows the values of compositional dissimilarity, the upper triangle shows the total number of species that are shared between each pair of areas and the main diagonal shows the total number of species of each area.

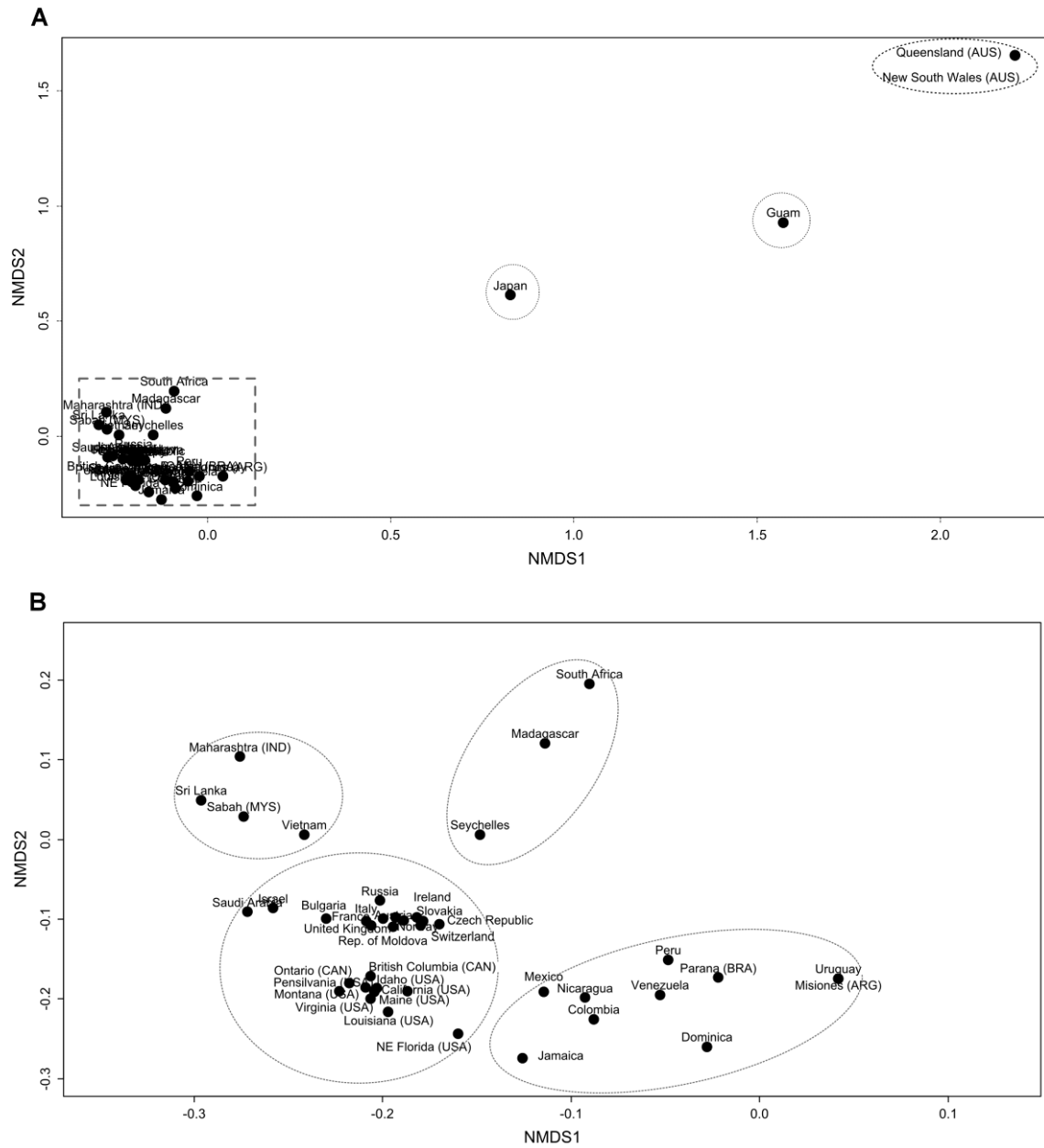


Fig. S5. Non-metric multidimensional scaling (NMDS) ordination of β_{sim} distance matrices for lists of species in their native ranges (**A**). The bottom plot (**B**) shows the relative location of the study areas that group close to each other (delimited by a grey dashed rectangle in the upper plot). Dotted grey ellipses were drawn by hand, highlighting biogeographical groupings mentioned in the text.

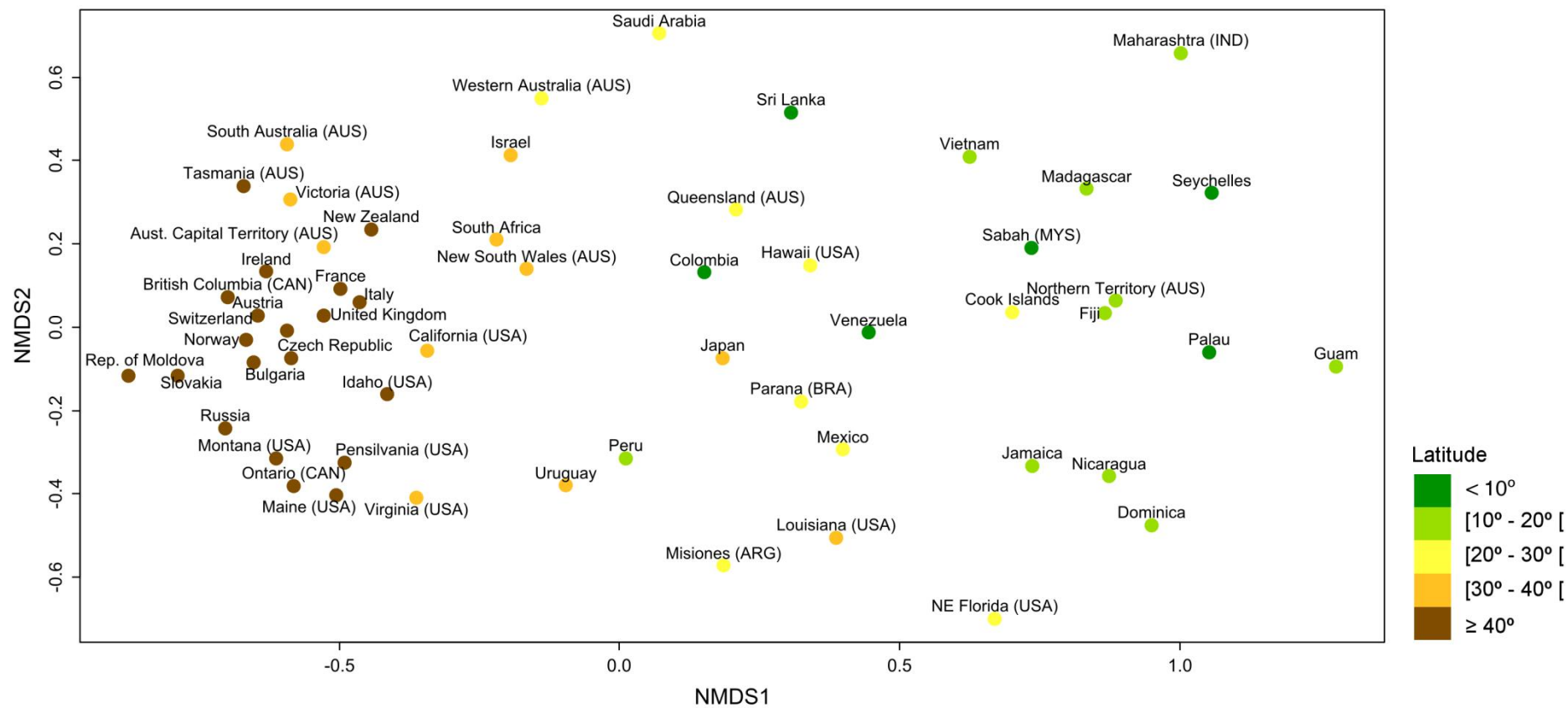


Fig. S6. Non-metric multidimensional scaling (NMDS) ordination of β_{sim} distance matrices for lists of species in their current ranges. Colour differences indicate the mean latitude of each location after reclassification into 10-degree latitude bands.

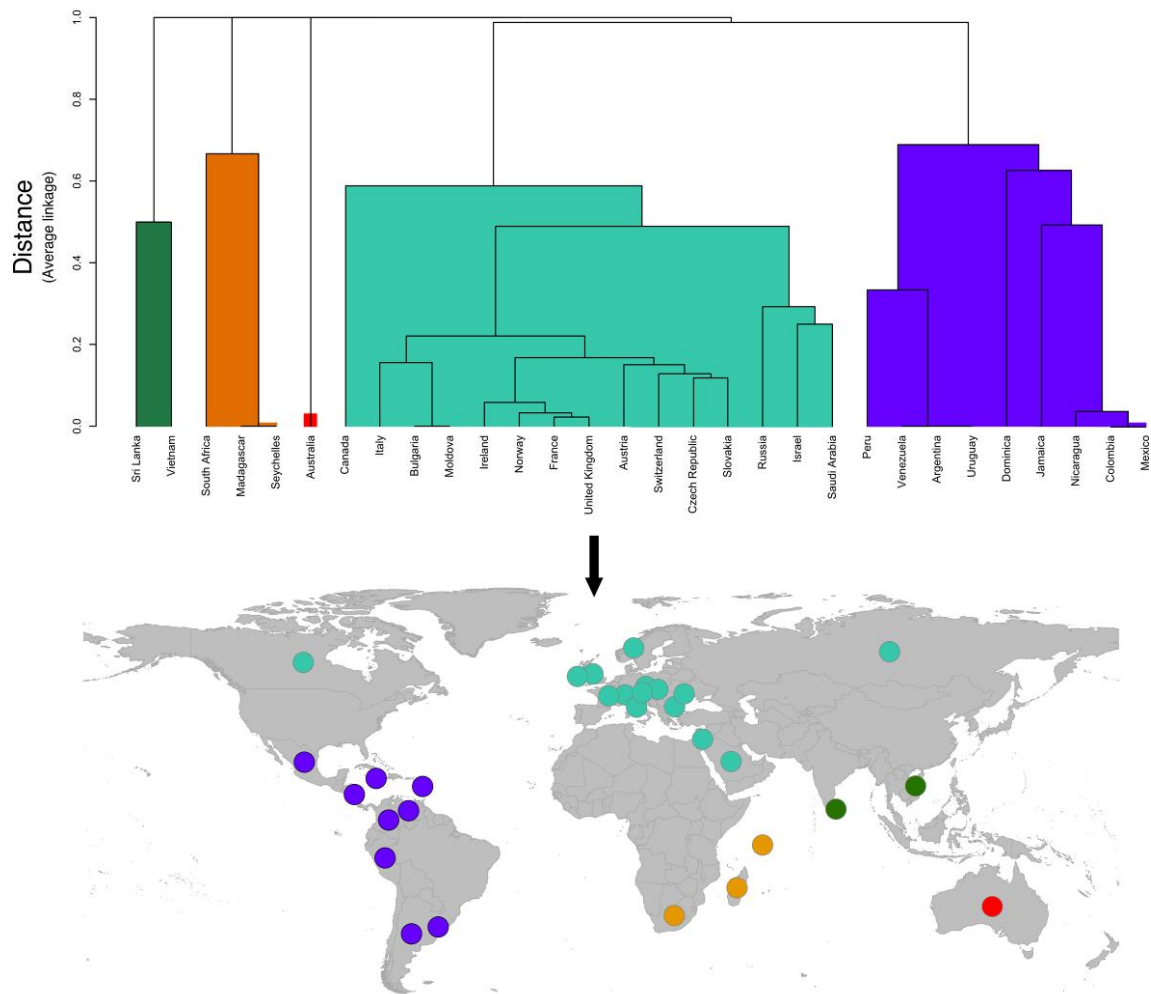


Fig. S7. Dendrogram and spatial clusters of the unweighted pair-group method using arithmetic averages (UPGMA) for β_{sim} distance matrices of country-level lists of species in their native ranges.

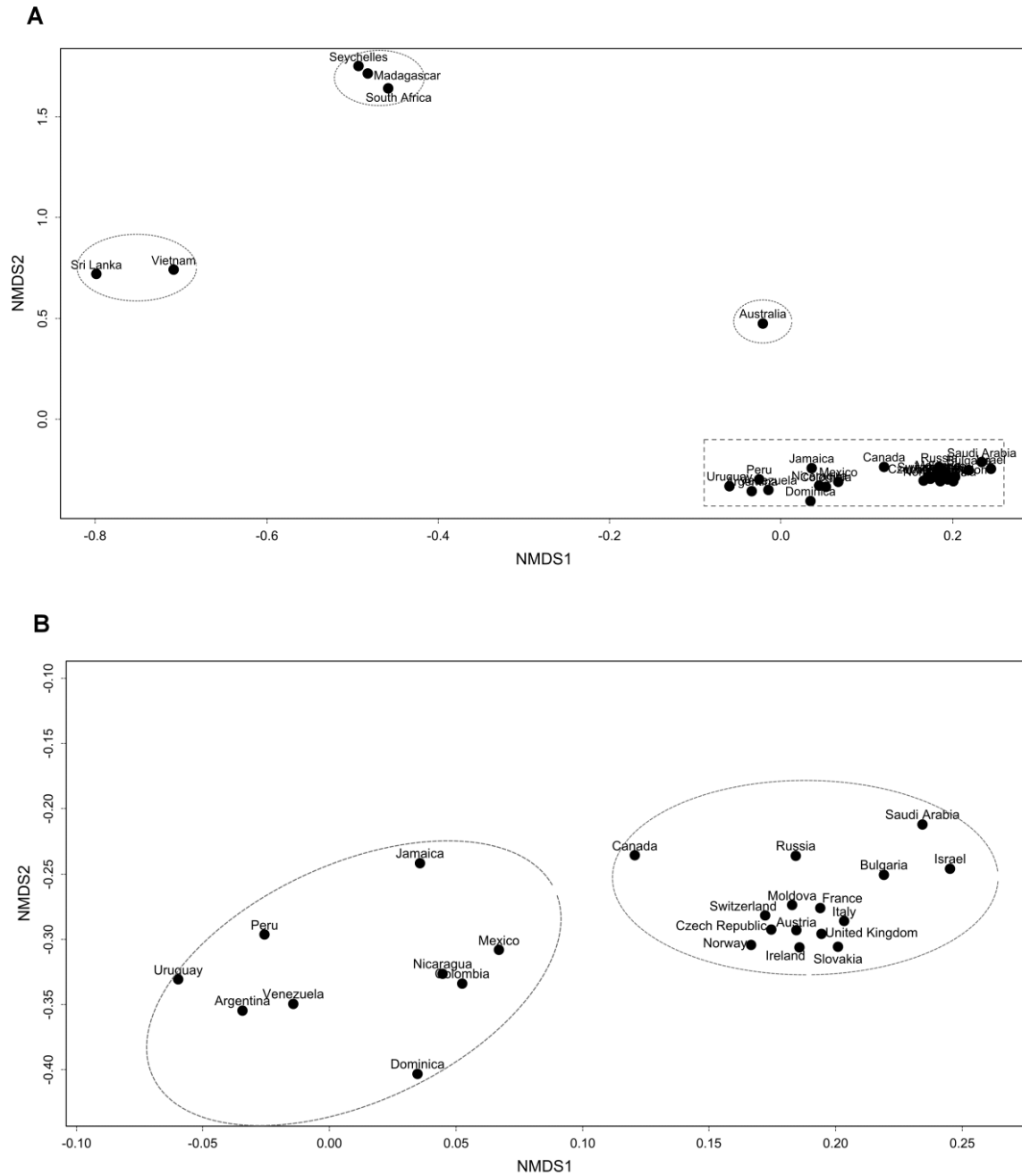


Fig. S8. Non-metric multidimensional scaling (NMDS) ordination of β_{sim} distance matrices for country-level lists of species in their native ranges (A). The bottom plot (B) shows the relative location of countries that group close to each other (grey dashed area in upper plot). Dotted grey ellipses were drawn by hand, highlighting biogeographical groupings mentioned in the text.

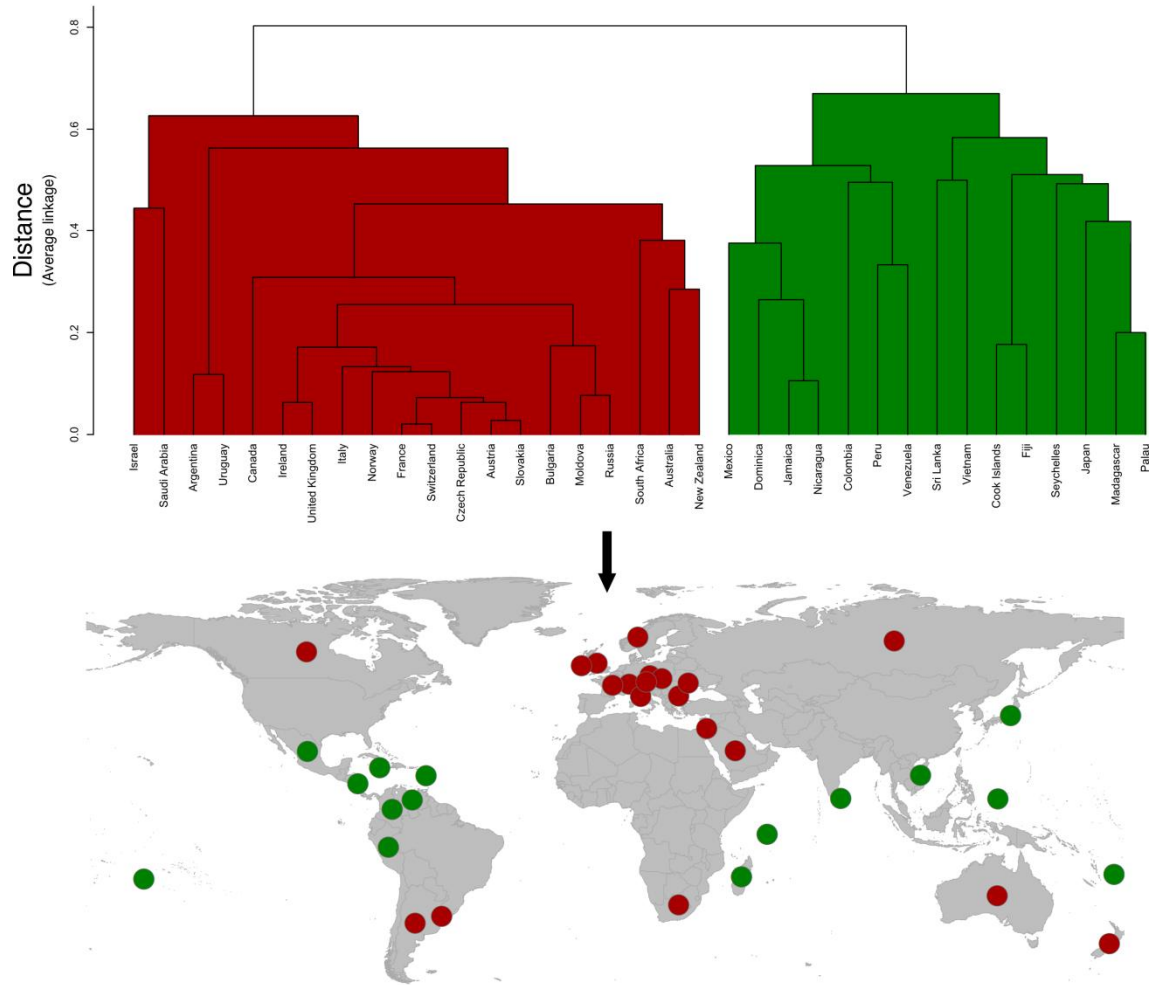


Fig. S9. Dendrogram and spatial clusters of the unweighted pair-group method using arithmetic averages (UPGMA) for β_{sim} distance matrices of country-level lists of species in their current ranges.

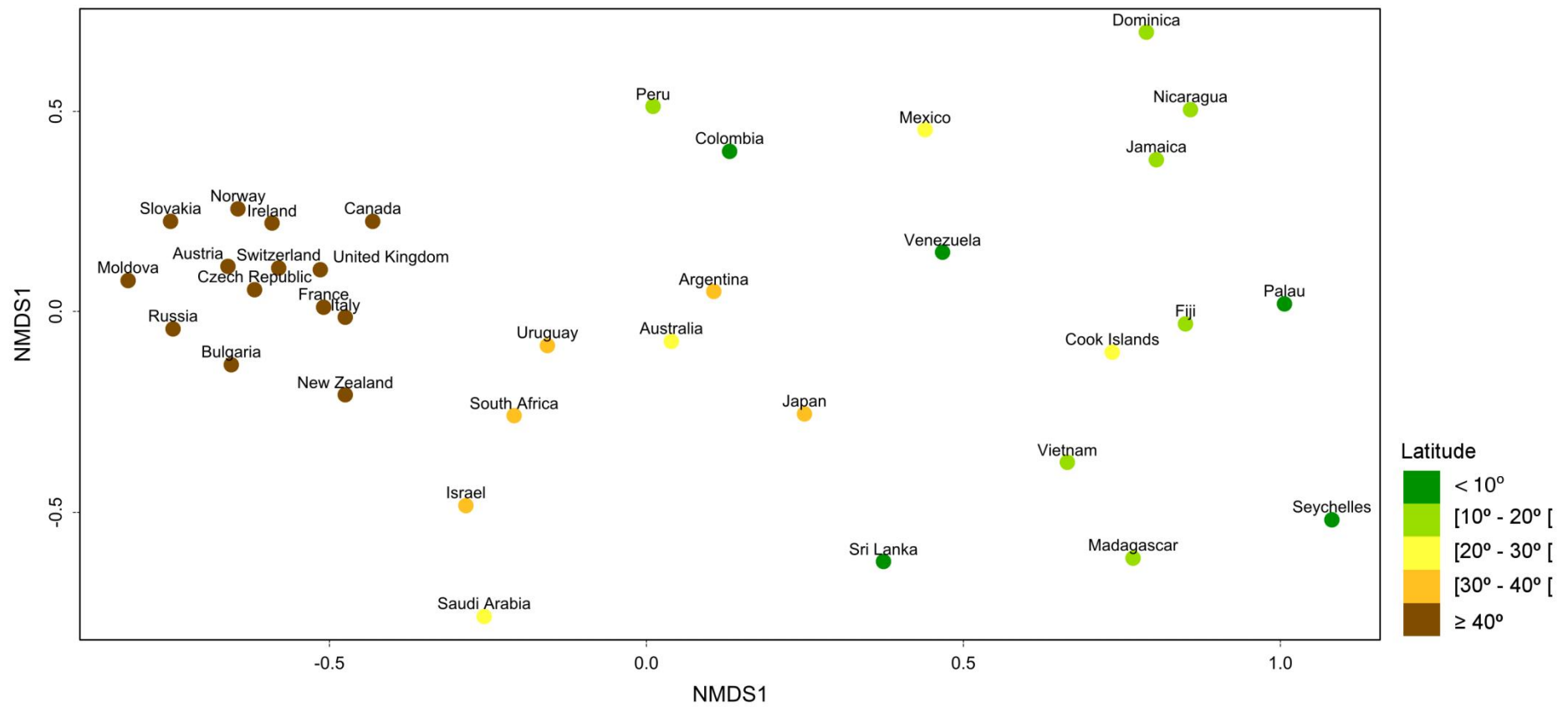


Fig. S10. Non-metric multidimensional scaling (NMDS) ordination of β_{sim} distance matrices for country-level lists of species in their current ranges. Colour differences indicate the mean latitude of each location after reclassification into 10-degree latitude bands.

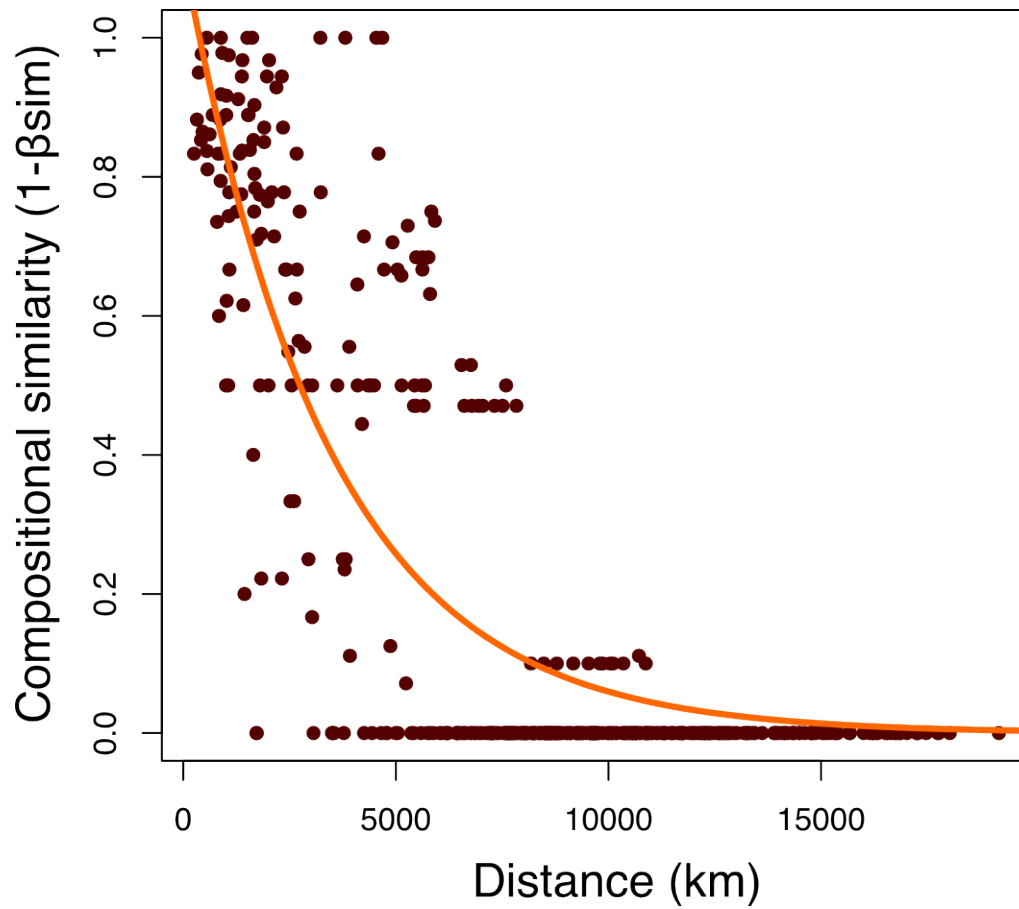


Fig. S11. Relationship between geographical distances and compositional similarities (measured as $1-\beta_{\text{sim}}$) of lists of alien terrestrial gastropods in native ranges based on country-level data. These data comprise 435 unique pairs of 30 countries. Model fit of exponential decay of compositional similarity with increasing distance is shown (orange). Exponential decay rate of compositional similarity per 1000 km = -0.29, $P < 0.001$. Significance was obtained by comparison with distribution of coefficients generated from 1000 permutations of the matrix of compositional similarities.

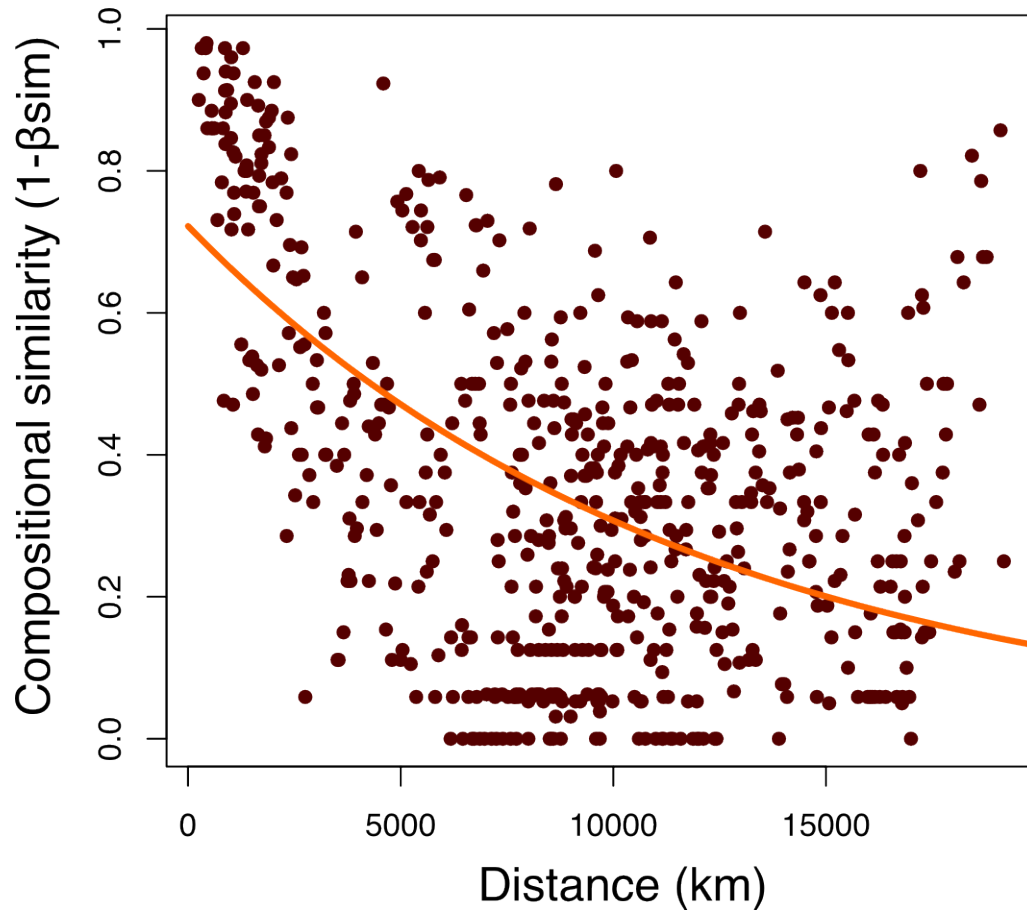


Fig. S12. Relationship between geographical distances and compositional similarities (measured as $1-\beta_{sim}$) of lists of alien terrestrial gastropods in current ranges based on country-level data. These data comprise 595 unique pairs of 35 countries. Model fit of exponential decay of compositional similarity with increasing distance is shown (orange). Exponential decay rate of compositional similarity per 1000 km = -0.09, $P < 0.001$. Significance was obtained by comparison with distribution of coefficients generated from 1000 permutations of the matrix of compositional similarities.

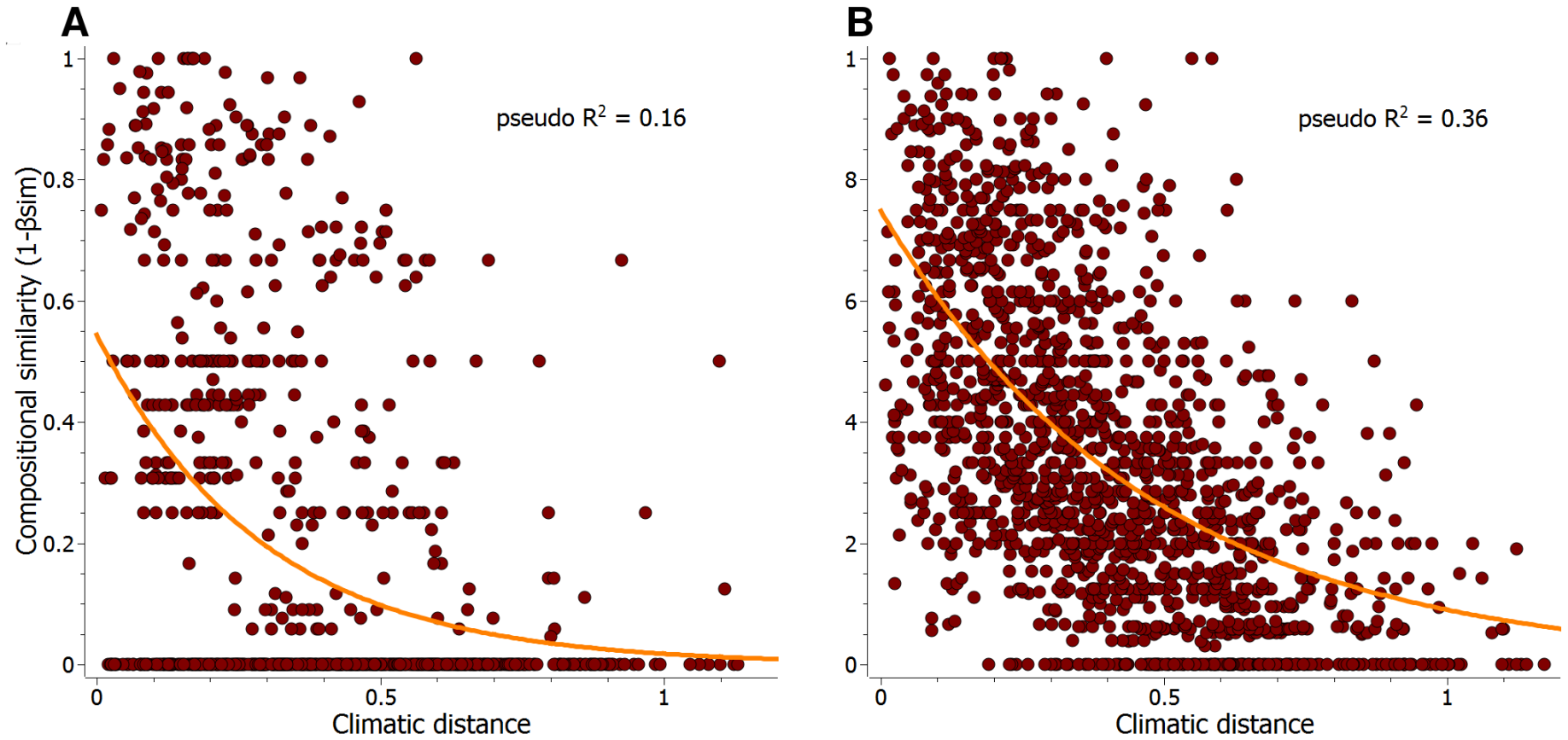


Fig. S13. Relationship between compositional dissimilarities and climate. **(A)** For species in native ranges. **(B)** For species in current ranges. The climatic predictor corresponds to Euclidean distances on scaled values (from 0 to 1) of mean annual temperatures and total annual precipitation. Model fits of exponential decay of compositional similarity with increasing climatic distance are shown (orange).

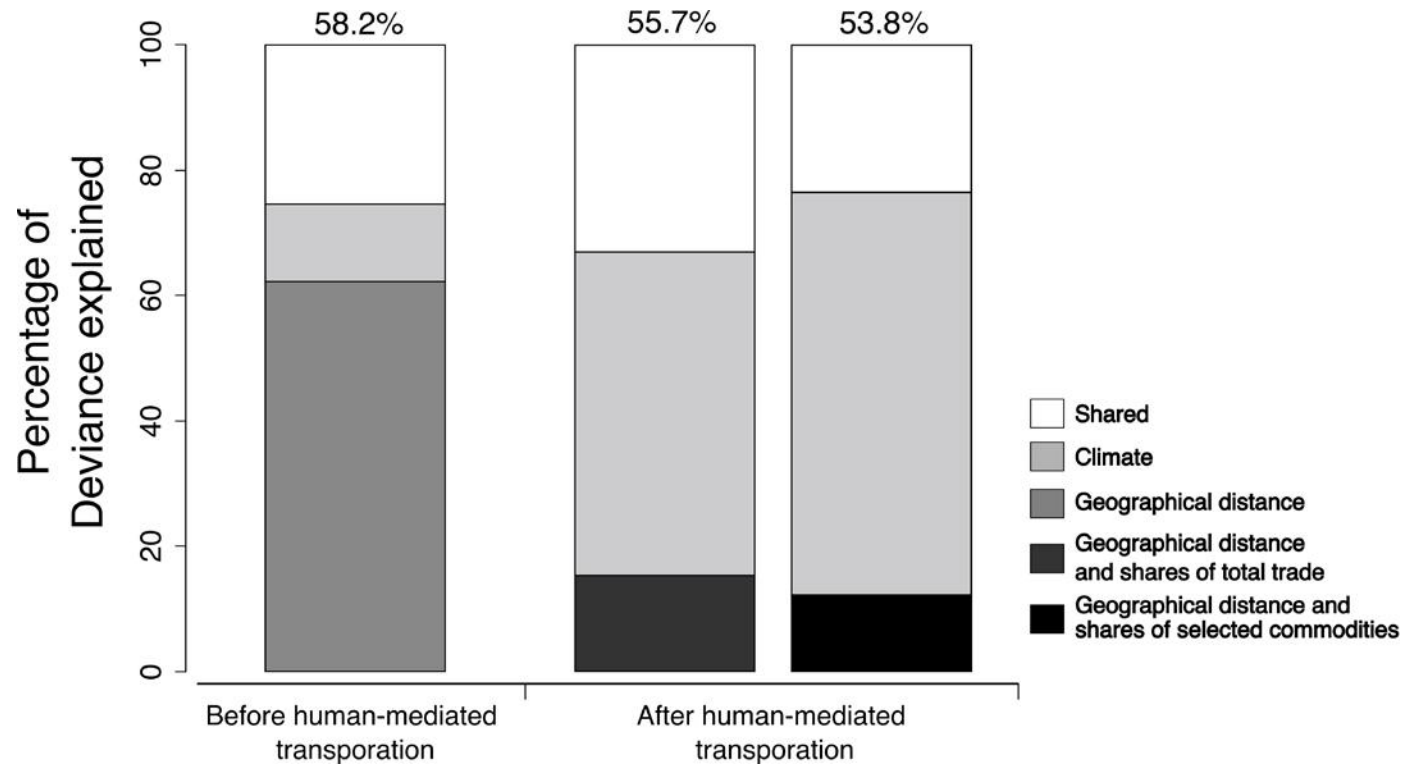


Fig. S14: Proportion of deviance explained in compositional dissimilarity of lists of alien terrestrial gastropods based on observations weighted by country extent. Proportions are shown for species in native ranges (i.e. before being dispersed by humans; left bar) and for species in current ranges (i.e. after being dispersed by humans; middle and right bars) and represent deviance that is i) jointly explained by climate and dispersal-related predictors (white), ii) explained by climate (lighter grey), iii) by geographical distance (representing natural dispersal; mid-grey), and iv) by natural and anthropogenic dispersal combined (darker grey and black). Percentages of total deviance in compositional dissimilarity explained by the full model are shown above each bar.

Table S1. List of references used for assembling a global database on the distribution of alien terrestrial gastropods.

Location	Data source
Argentina	° A. Rumi, J. Sánchez, N. S. Ferrando, <i>Theba pisana</i> (Müller, 1774) (Gastropoda, Helicidae) and other alien land molluscs species in Argentina. <i>Biol. Invasions</i> 12 , 2985-2990 (2010).
Australia (including: Australian Capital Territory; New South Wales; Northern Territory; Queensland; South Australia; Tasmania; Victoria; Western Australia)	° ABRS, <i>Australian Faunal Directory</i> (Australian Biological Resources Study, Canberra, 2009).
Austria	° F. Essl, W. Rabitsch, <i>Neobiota in Österreich</i> . (Umweltbundesamt Wien, 2002).
Bulgaria	° A. Irikov, Z. Eross, An updated and annotated checklist of Bulgarian terrestrial gastropods (Mollusca: Gastropoda). <i>Folia Malacol.</i> 16 , 199-206 (2008).
California (USA)	° B. Roth, P. S. Sadeghian, <i>Checklist of the land snails and slugs of California</i> . (Santa Barbara Museum of Natural History, 2006).
Canada (including British Columbia and Ontario)	° F. W. Grimm, R. G. Forsyth, F. W. Schueler, A. Karstad, <i>Identifying Land Snails and Slugs in Canada: Introduced Species and Native Genera</i> . (Canadian Food Inspection Agency, Quebec, 2010). [List with updates provided by R. G. Forsyth: <i>Aegopinella nitidula</i> (Canada; BC); <i>Arianta arbustorum</i> (Canada; ON); <i>Arion ater</i> (s.l.) (Canada); <i>Arion ater</i> (s.s.) (Canada); <i>Arion circumscriptus</i> (Canada; BC); <i>Arion distinctus</i> (Canada); <i>Arion fasciatus</i> (s.l.) (Canada; ON); <i>Arion fasciatus</i> (s.s.) (Canada; BC; ON); <i>Arion fuscus</i> (Canada; BC; ON); <i>Arion hortensis</i> (s.l.) (Canada); <i>Arion hortensis</i> (s.s.) (Canada; BC; ON); <i>Arion intermedius</i> (Canada; BC; ON); <i>Arion rufus</i> (Canada; BC; ON); <i>Arion silvaticus</i> (Canada; BC; ON); <i>Arion subfuscus</i> (Canada; ON); <i>Boettgerilla pallens</i> (Canada; BC); <i>Carychium minimum</i> (Canada; BC; ON); <i>Carychium tridentatum</i> (Canada; BC); <i>Ceciloides acicula</i> (Canada; ON); <i>Cepaea hortensis</i> (ON); <i>Cepaea nemoralis</i> (Canada; BC; ON); <i>Cornu aspersum</i> (Canada; BC); <i>Deroceras invadens</i> (Canada; BC; ON-uncertain); <i>Deroceras reticulatum</i> (Canada; BC; ON); <i>Discus rotundatus</i> (Canada; BC; ON); <i>Lauria cylindracea</i> (Canada; BC); <i>Lehmannia marginata</i> (Canada); <i>Lehmannia valentiana</i>

	(Canada; BC; ON); <i>Limacus flavus</i> (Canada; BC); <i>Limax maximus</i> (Canada; BC; ON); <i>Oxychilus alliarius</i> (Canada; BC; ON); <i>Oxychilus cellarius</i> (Canada; BC; ON); <i>Oxychilus draparnaudi</i> (Canada; BC; ON); <i>Patera appressa</i> (Canada; ON); <i>Succinella oblonga</i> (Canada; ON); <i>Testacella haliotideia</i> (Canada; BC); <i>Trochulus hispidus</i> (Canada; ON); <i>Trochulus striolatus</i> (Canada; BC; ON); <i>Vallonia excentrica</i> (BC); <i>Vallonia pulchella</i> (BC); <i>Vitrea contracta</i> (Canada; BC; ON); <i>Xerolenta obvia</i> (Canada; ON)]
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Table S2. Sensitivity of values of compositional dissimilarity to random errors in the data sets. Results correspond to the Pearson correlation coefficient between values of compositional dissimilarities calculated from the original data sets with values calculated from datasets with random permutation of species or region records. Full permutation of records was performed for individual species and regions and for random selections of 5, 10, and 15% of all species and of all regions. Mean correlation values are based on 100 repetitions of the error simulations. Based on randomization tests all correlations were significant at $P < 0.001$.

Data set	Species								Region							
	1		5%		10%		15%		1		5%		10%		15%	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Native distributions in countries and sub-national entities	0.993	0.015	0.921	0.059	0.835	0.063	0.754	0.069	0.978	0.01	0.945	0.009	0.897	0.014	0.828	0.024
Current distributions in countries and sub-national entities	0.997	0.003	0.97	0.015	0.945	0.02	0.926	0.088	0.975	0.009	0.934	0.02	0.855	0.024	0.781	0.025
Native distributions in countries	0.991	0.002	0.864	0.072	0.806	0.055	0.739	0.047	0.956	0.016	0.924	0.027	0.875	0.088	0.77	0.04
Current distributions in countries	0.997	0.004	0.976	0.022	0.955	0.015	0.929	0.02	0.962	0.015	0.912	0.017	0.853	0.018	0.798	0.042

Table S3. Co-phenetic correlations (r) for the dendrograms of unweighted pair-group method using arithmetic averages (UPGMA); weighted pair-group method using arithmetic averages (McQuitty's method) and Ward's method (minimum variance).

Method	National and subnational regions		Countries only	
	Native ranges	Current ranges	Native ranges	Current ranges
UPGMA	$r = 0.91$	$r = 0.82$	$r = 0.95$	$r = 0.85$
McQuitty	$r = 0.86$	$r = 0.78$	$r = 0.94$	$r = 0.79$
Ward	$r = 0.64$	$r = 0.66$	$r = 0.78$	$r = 0.75$

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