Unimodal Latitudinal Pattern of Land-Snail Species Richness across Northern Eurasian Lowlands

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Abstract

Large-scale patterns of species richness and their causes are still poorly understood for most terrestrial invertebrates, although invertebrates can add important insights into the mechanisms that generate regional and global biodiversity patterns. Here we explore the general plausibility of the climate-based “water-energy dynamics” hypothesis using the latitudinal pattern of land-snail species richness across extensive topographically homogeneous lowlands of northern Eurasia. We established a 1480-km long latitudinal transect across the Western Siberian Plain (Russia) from the Russia-Kazakhstan border (54.5° N) to the Arctic Ocean (67.5° N), crossing eight latitudinal vegetation zones: steppe, forest-steppe, subtaiga, southern, middle and northern taiga, forest-tundra, and tundra. We sampled snails in forests and open habitats each half-degree of latitude and used generalized linear models to relate snail species richness to climatic variables and soil calcium content measured in situ. Contrary to the classical prediction of latitudinal biodiversity decrease, we found a striking unimodal pattern of snail species richness peaking in the subtaiga and southern-taiga zones between 57 and 59° N. The main south-to-north interchange of the two principal diversity constraints, i.e. drought stress vs. cold stress, explained most of the variance in the latitudinal diversity pattern. Water balance, calculated as annual precipitation minus potential evapotranspiration, was a single variable that could explain 81.7% of the variance in species richness. Our data suggest that the “water-energy dynamics” hypothesis can apply not only at the global scale but also at subcontinental scales of higher latitudes, as water availability was found to be the primary limiting factor also in this extratropical region with summer-warm and dry climate. A narrow zone with a sharp south-to-north switch in the two main diversity constraints seems to constitute the dominant and general pattern of terrestrial diversity across a large part of northern Eurasia, resulting in a subcontinental diversity hotspot of various taxa in this zone.

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Introduction

The overall decline in species diversity with increasing latitude is one of the most prominent features of the natural world (e.g. [1], [2], [3], [4]), but the causes of this gradient remain insufficiently explained in spite of many hypotheses proposed and extensive discussions (e.g. [5], [6], [7]). Previous research was biased to some taxa and regions, and little evidence still exists for terrestrial invertebrates (e.g. [2], [8]). While recent studies stress the greater importance of climate than geographical location (e.g. [9], [10]), the mechanisms by which latitudinal variation in climate determines species numbers are still poorly understood ([7], [11]). As latitude correlates with a number of interacting and intercorrelated environmental gradients (e.g. temperature, precipitation, seasonality, evapotranspiration), direct tests of the hypotheses are difficult and can be controversial ([2]). Although most studies have recognized the “classical” pattern of decreasing species richness towards the poles, both positive and unimodal relationships were repeatedly revealed in several taxa (see [2]). These exceptions were found to be scale dependent. Almost all positive relationships were found across small latitudinal extents (<20° latitude), being associated with regional patterns of heterogeneity in local topography, geology, hydrology, or historical factors ([22]).

In contrast, unimodal relationships with a mid-latitudinal peak of diversity were all but one found across broad extents (>20° latitude). The examples came mostly from studies of terrestrial insects (e.g. [12], [13]), but there is also evidence for aquatic invertebrates, herbs, marine and terrestrial birds, and mammals (e.g. [11], [14]). Several explanations were suggested, e.g. mid-latitude peak in host density ([13]), mid-domain effect ([13]), habitat specificity ([12]), topographical heterogeneity ([16]) or an increase in resources ([14]). Although the mechanism underlying such unimodal patterns remain poorly known, hardly any doubt exists that climate influences large-scale patterns of species richness. The climatically based “energy hypothesis” has been postulated in several versions and received a considerable attention over the last three decades (e.g. [11], [17], [18]).

In this study we focus on land snails, an invertebrate taxon with as yet poorly explored patterns of latitudinal diversity. Land snail diversity across large scales can be climatically controlled by two principal ecological factors, winter temperature and moisture. Many land snail species apparently do not have any cryoprotective
Land-Snail Species Richness across Northern Eurasia

Study area and sites

We studied land snail species richness across a latitudinal transect from the northern steppe zone at the Russia-Kazakhstan border SW of the city of Omsk at 54.5°N to the southern tundra zone at the Arctic Ocean coast near the town of Tazovskiy at 67.5°N (Fig. 1). The straight-line distance between the southernmost and northernmost site was 1480 km. This transect crossed seven latitudinal vegetation zones ([32]): 1. steppe zone, dominated by grasses such as Stipa and Festuca, with rare occurrence of small woodland and shrubland patches in terrain depressions; 2. forest-steppe zone, consisting of a mosaic of dry to mesic grasslands at the flatland and small open woodlands dominated by birches (Betula pendula and B. pubescens) and aspen (Populus tremula) with many temperate light-demanding species in the herb layer, occurring in shallow terrain depressions; 3. subtaiga zone, dominated by forests with birches and aspen, with locally admixed fir (Abies sibirica) and lime (Tilia cordata), and Scots pine (Pinus sylvestris) on sandy soils, with a herb layer composed mainly of temperate forest herbs; wet and mesic grasslands occur in scattered patches in a predominantly forested landscape; 4. southern taiga zone, with the same trees as in the subtaiga zone, but with an additional occurrence of spruce (Picea abies) and Siberian pine (Pinus sibirica); grasslands disappear from the landscape, and patches of deep bogs with open low growing stands of Scots pine appear; 5. middle taiga zone, consisting of a mosaic of coniferous forests with Siberian pine and spruce (on loamy soils) or Scots pine (on sandy soils), frequent occurrence of birch (Betula pubescens) and extensive deep bogs; the herb layer of forests is dominated by boreal shrub shrubs and herbs, bryophytes and lichens; 6. northern taiga zone, a mosaic of forests with Siberian pine, Scots pine, larch (Larix sibirica), spruce and birch (Betula pubescens) on permafrost, and shallow bogs including palsa; 7. forest-tundra zone, semi-open landscape with patches of larch woodlands, extensive stands of dwarf birch (Betula nana), grasslands, mires and willow scrub at wet sites; 8. tundra zone, a treeless landscape with herbaceous and dwarf shrub vegetation, dwarf birch stands, mires and willow scrub.

The whole transect run across the flatland of the West Siberian Plain, ranging in altitude from 148 m (in the south) to 4 m a.s.l. (in the north). Soils were loamy from the steppe zone to the south of the middle taiga zone, and also in the forest-tundra and tundra zones. In contrast, across most of the middle and northern taiga zones soils were predominantly sandy. According to the World-Clim dataset ([33]), mean January temperature ranged from –17°C (in the south) to –26°C (in the north) and mean July temperature from 20°C to 13°C. Annual precipitation ranged from 360 mm (in the south) to 570 mm (in the middle taiga zone).

Sampling sites (n = 29) were placed systematically along the transect, with one site each half degree of latitude. Only in the northernmost part, four sites were spaced by a quarter degree in order to capture the rather narrow zone of forest-tundra. Disturbed sites such as arable land, areas affected by oil or gas extraction or roadsides were avoided. Large river floodplains were avoided too in order to focus on zonal habitats. In some cases, it was necessary to shift the sampling site slightly to the north or south from the target latitude to avoid disturbed sites, floodplains or to sample both forest and open habitats at the same site. However, these shifts were never larger than 5 minutes of latitude.

Species sampling

At each site we randomly chose three squared sampling plots of 100 m² representing locally predominant habitat types at the site. Because at most sites overall habitat heterogeneity was very low, represented by few homogeneous habitats of large spatial extent, the three plots were sufficient to cover the main habitat heterogeneity. At some sites we had enough time to sample one or two additional plots, which resulted in four and five plots sampled at seven and two sites, respectively (Table 1). This gave a total of 98 plots investigated. In all plots snails were sampled by a single person (M. Horsák). To record as complete inventory of snail assemblage of each plot as possible, various sampling techniques were applied depending on the habitat type investigated. At non-wetland habitats, snails were carefully searched by eye in all microhabitats of the plot for one hour. At species-poor sites (e.g. dry steppes on loess) the sampling was stopped when all recorded species were represented by more than two individuals and at the same time no other species was found for ca. 15 minutes (but sampling was never shorter than 30 minutes). The same stopping rules were used in richer habitats, where sampling took longer time, but not longer than another 30 minutes (in cases of the richest forest plots in the southern taiga). In damper habitat
Figure 1. Study area with the position of 29 sampling sites along the transect.
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types, i.e. mires, fens and wet tundra, a 121 sample of the top layer of the ground surface including topsoil, litter, bryophytes and herbaceous vegetation was collected and processed in the field using the wet sieving method ([34]). All recorded shells and live-shelled snails were collected and kept dry. Few recorded individuals of slugs were preserved in 70% ethanol. Samples were identified under a dissecting microscope in the laboratory using available identification literature ([35], [36], [37], [38]) and the first author’s comparative collection of Siberian samples. Nomenclature mainly follows [39], but [35] and [37] were used for species of non-European distribution. We declare that no permission was needed as the samples were not collected on privately owned or protected lands and no legally protected species were sampled.

Explanatory variables

For each site, annual precipitation sum and mean January and July temperature were obtained from the WorldClim database ([33], www.worldclim.org) using the ArcGIS 8.3 program (www.esri.com). Annual potential evapotranspiration, calculated from the WorldClim data, was obtained from the website of CGIAR-CSI Consortium for Spatial Information (http://csi.cgiar.org/Ariddity/, [39]). We also expressed water balance as the difference between annual precipitation sum and annual potential evapotranspiration ([40]). As land snail species richness and composition is tightly related to calcium availability (e.g. [41]), we also measured calcium (Ca) content in topsoil (or in peat in mires). Although the amount of calcium is strongly correlated with climate due to higher cation leaching in wetter conditions, any heterogeneity in local geology and vegetation cover ([42]) can have positive effects on snail species richness. Therefore we collected soil samples from the mineral topsoil horizon at a depth of 5–10 cm in four places within each plot. These four subsamples were mixed and sieved at a mesh size of 1 mm. Available calcium was extracted from the sieved soil using the Mehlich III method (strong acid extraction with ion complex) and determined by atomic absorption spectrophotometry (AAS 933 Plus, GBC Scientific Equipment, Melbourne, Australia). The analysis was done by AgroLab, Troubsko, Czech Republic according to the methods described by [43].

Statistical analyses

All basic data used in the analyses and the graphs are provided in Table S1. Correlations among explanatory variables were inspected graphically (Figs. S1 and S2) and quantified using the Spearman correlation coefficient. As tight correlations were found among mean annual temperature, mean July and January temperature (Fig. S1), we used only January temperature as the most ecologically relevant measure of temperature for land snails due to a poorly evolved cold-hardiness within this taxon ([20]).

For each of 29 sampling sites we calculated mean number of species recorded at all plots of a site (\(\bar{S}\), \(\bar{n}\)), and within this zone an increase in the number of species was observed from the middle taiga to the northern taiga zone. At the transition to the forest-tundra zone (Fig. 2A). The number of species started at the transition between southern taiga and middle taiga and continued throughout the latter zone (Fig. 2A). The number of species was linearly decreasing with temperature and soil calcium content (Fig. 2B). Harsh conditions, strengthened by the presence of sandy soils, kept the number of species very low from the northern margin of the middle taiga zone across the whole of the northern taiga zone. At the transition to the forest-tundra zone and within this zone an increase in the number of species was found, likely associated with the increase in calcium content in the soils (Figs. 2B and S2). However, in the tundra zone the number of species linearly dropped down to zero.

Water balance was the single variable that expressed a tight relationship with species richness along the whole latitudinal extent (Fig. 3D). Using a generalized linear model we found highly significant quadratic response of the mean number of species to water balance. This single predictor was able to explain 81.7% of the total variance in mean numbers of species (quasi-GLM-p, \(p<0.001\)). The most parsimonious model (with water balance not included, see Methods) consisted of annual precipitation (linear
| Species/Latitude ('N) | 54.5 | 55.0 | 55.5 | 56.0 | 56.5 | 57.0 | 57.5 | 58.0 | 58.5 | 59.0 | 59.5 | 60.0 | 60.5 | 61.0 | 61.5 | 62.0 | 62.5 | 63.0 | 63.5 | 64.0 | 64.5 | 65.0 | 65.5 | 66.0 | 66.5 | 67.0 | 67.25 | 67.5 |
|----------------------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| Vallonia pulchella (Müller) | +   | +   | +   | +   | +   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   |
| Vallonia costata (Müller) | +   | +   | +   | +   | +   | +   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   |
| Cochlicopa lutaricella (Porro) | +   | +   | +   | +   | +   | +   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   |
| Nesovitrea hammonis (Strom) | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   |
| Succinella oblonga (Draparnaud) | -   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   |
| Derceras altaicum (Simroth) | -   | +   | +   | +   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   |
| Zonitides nitidus (Müller) | -   | +   | +   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   |
| Fundicium pygmaeum (Draparnaud) | -   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   |
| Eucnalous fulvus (Müller) | -   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   |
| Vertigo antivertigo (Draparnaud) | -   | -   | +   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   |
| Vertigo pygmaea (Draparnaud) | -   | -   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   |
| Eucnalous pratcica (Reinhardt) | -   | -   | +   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   |
| Vitrina pellucida (Müller) | -   | -   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   |
| Fruticola schrenckii (Middendorff) | -   | -   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   |
| Discus ruderatus (Hartmann) | -   | -   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   |
| Carychium minimum Müller | -   | -   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   |
| Oxyloma elegans (Risso) | -   | -   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   |
| Vertigo angustior Jeffrey | -   | -   | +   | +   | +   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   |
| Vertigo substriata (Jeffrey) | -   | -   | +   | +   | +   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   |
| Columella edentula (Draparnaud) | -   | -   | +   | +   | +   | +   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   |
| Vertigo pusilla Müller | -   | -   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   | +   |
### Table 1. Cont.

| Species/Latitude (°N) | 54.5 | 55.0 | 55.5 | 56.0 | 56.5 | 57.0 | 57.5 | 58.0 | 58.5 | 59.0 | 59.5 | 60.0 | 60.5 | 61.0 | 61.5 | 62.0 | 62.5 | 63.0 | 63.5 | 64.0 | 64.5 | 65.0 | 65.5 | 66.0 | 66.5 | 67.0 | 67.5 |
|-----------------------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| Cochlicopa lubrica (Müller) | -     | -     | -     | -     | -     | +     | +     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| Succinea putris (Linne) | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| Nesovitrea petronella (Pfeiffer) | -     | -     | -     | -     | -     | +     | +     | +     | +     | +     | +     | -     | +     | +     | +     | +     | +     | +     | +     | +     | +     | +     | +     | +     | -     | -     | -     | -     |
| Vertigo ranneyensis (Westerlund) | -     | -     | -     | -     | -     | -     | -     | -     | +     | +     | +     | +     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| Arion fuscus (Müller) | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| Vertigo aff. gouldi Binney | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| Vertigo modesta aff. hoppii (Müller) | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| Deroceras laeve (Müller) | -     | -     | -     | -     | -     | -     | -     | +     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| Zoogenetes harpa (Say) | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| Vertigo liljeborgii (Westerlund) | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | +     | -     | -     | -     | -     | -     | -     | -     | -     |
| *Vertigo extima* (Westerlund) | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | (h) | -     | -     | -     |
| Total no. of plots | 5     | 4     | 3     | 4     | 3     | 3     | 3     | 3     | 3     | 3     | 3     | 4     | 3     | 3     | 4     | 3     | 4     | 3     | 4     | 3     | 3     | 3     | 3     | 3     | 3     | 3     | 3     | 3     |
| Total no. of species | 4     | 8     | 11    | 7     | 11    | 16    | 15    | 9     | 15    | 10    | 8     | 8     | 9     | 5     | 3     | 1     | 1     | 2     | 5     | 0     | 2     | 1     | 1     | 1     | 6     | 3     | 3     | 2     | 0     |

*this species was recorded at the site but not in the studied plots.

Individual zones (from left to right): steppe, forest-steppe, subtaiga, southern taiga, middle taiga, northern taiga, forest-tundra, and tundra, indicated using alternating bold style. Presence of a species is marked by crosses; species are ordered based on their first finding along the transect from south to north.

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and quadratic term), mean January temperature (linear term), soil calcium content (linear term) and interaction between the quadratic term of annual precipitation and soil calcium. The model explained 87.3% of the total variance in species richness (quasi-GLM-p, p < 0.001).

Discussion

Our data suggest a climatically controlled unimodal pattern of latitudinal land snail diversity across Western Siberia. Previous reports of unimodal diversity pattern along latitude originated from larger spatial extents ([12, 13, 16]) and were explained by various mechanisms, although climatically related. The pattern observed for land snails in Western Siberia was controlled by two main climatic constraints that were, however, operating at different latitudes: drought stress in the south and cold stress in the north. Hawkins et al. [11] analysed global diversity of terrestrial birds and found that linear association of climate with species richness at continental extents is rather exceptional. The data from the former USSR reported in their study (see Figure six in [11]) suggest the same unimodal pattern as we found for land snail diversity, with a peak in the subtaiga and southern taiga zones. A similar pattern was also shown for amphibians (Figure one in [47]), which seems to be more prominent towards the western Palaearctic. As we observed the same pattern along the studied transect also for vascular plant diversity (unpubl. data), which partly coincides with the coarse-scale map of plant species numbers per 1000 km² ([48]), the climatically driven latitudinal change in diversity seems to be universal for this part of Eurasia. However, the mechanisms shaping these unimodal diversity changes can differ among individual taxa. With a high certainty
we can reject Rosenzweig’s ([49]) “habitat heterogeneity” hypothesis, likely explaining a unimodal latitudinal pattern of plant diversity in continental Chile ([16]), as the observed changes in the number of land snail species in Western Siberia occurred on flatland, in absence of any significant topographical variance along the transect (elevation of studied plots along the whole transect varied between 148 and 4 m a.s.l.).

There was no clear relation between the heterogeneity of habitat types in the landscape and local species richness at particular sites, either mean or cumulative. We found southern taiga zone to be the richest in species, although the landscape was dominated by a single habitat type, mixed broadleaf-conifer hemiboreal forest. Among forest assemblages, compositional pattern was nested, with species accumulating towards the southern taiga zone from both latitudinal directions. However, the diversity pattern was notably different between forest and open habitats. Open habitat types changed more dramatically than forest types with latitude, continuously replacing one another along the transect, from dry steppe through mesic and wet grasslands and bogs to herbaceous and shrubby tundra. This constituted a considerable compositional turnover with no shared snail species for the steppe and tundra zones. This difference also explains why the cumulative numbers of species recorded in all forest and open plots were not much different, despite often high differences in the numbers for individual plots.

The observed changes in species richness can possibly result from different colonization histories along the transect. However, there are no obvious geographical barriers for land snails that could hamper species migration as almost all recorded snails belong to minute species known as very effective passive dispersers (e.g. [50], [51]). Further, the whole area was ice-free during the last glacial maximum ([52]), so there was enough time for species to saturate all favourable habitats. Further, almost all recorded species have wide distributions (Holarctic, Palaeartic, Siberian) with ranges extending across the temperate and boreal zones of the continent. Thus, there seems to be no significant imprint of the postglacial colonization history in this part of Eurasia, as known from western and central Europe ([51], [53]).

We observed a sharp drop of species numbers with decreasing water availability in areas of high ambient energy that supports the “water-energy dynamics” hypothesis developed for plant diversity ([27], [29]). As the major predictions of this hypothesis were fulfilled also by the global diversity pattern of terrestrial birds, Hawkins et al. [11] suggested this hypothesis as a unifying hypothesis for terrestrial diversity gradients. It postulates that measures of ambient energy are the best predictors of diversity patterns in high-latitude regions, while water-related variables best explain diversity gradients in the subtropics and tropics, i.e. areas with high energy input ([30]). Our data suggest a broader plausibility of this prediction, as water availability can be the primary limiting factor also in extratropical regions with warm and dry climate. Although the ambient energy was proposed as the ultimate constraint for most terrestrial organisms above ca. 50°N (e.g. [17], [54]), we found the main interchange of the two principal diversity constraints (cold stress vs. drought stress) between 57 and 59°N. It seems to be a dominant and general

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Figure 3. Changes in mean numbers of land snail species in relation to four environmental variables.

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pattern of diversity across a great part of northern Eurasia, from Eastern Europe to Eastern Siberia (see Figure six in [11]). Water-related decrease in bird diversity from the southern taiga towards the dry steppe zone of Kazakhstan, Uzbekistan and Turkmenistan, occurs between 30° and 50° of latitude. Our transect ended at the northern margin of this zone, but further continuous decrease in diversity towards southern part of this warm and dry region is very likely. Dry steppes or saline habitats in this region typically contain no snails in small plots. The unimodal change in snail species richness, though caused by different limiting factors, is very well described by water balance, a variable describing moisture availability resulting from the counteracting effects of precipitation and evapotranspiration. However, a more complex model incorporating both precipitation and temperature as separate variables, accompanied with soil calcium, was able to explain slightly more variation in species data. Likewise, the balance of temperature and precipitation (included in both linear and quadratic terms) was the best overall predictor of the variation in global amphibian richness ([47]).

The question remains, however, which mechanism causes the decline of species richness from the mixed forests of southern taiga towards the north. Decreasing ambient energy can control diversity by low temperature stress (freezing) or low productivity that translates into lower availability of food and shelters for overwintering at higher latitudes. There is not only a strong collinearity but also a strong positive feedback between these two factors. In ecosystems with very cool winters, distribution of terrestrial snails is constrained by the lack of shelters for overwintering ([8]), which becomes more pronounced where herbaceous biomass production is low ([24]). Considering the known physiological constraints of land snails (e.g. [19]), low temperature stress is a more parsimonious explanation than the limited food availability. Some species frequently inhabiting low-productive steppe ecosystems (e.g. *Vallonia pulchella*) are not able to cope with open tundra habitats of similar productivity levels ([55]). The freezing intolerance hypothesis is also supported by a limited distribution of large-bodied species towards higher altitudes, as smaller species have better supercooling abilities ([20]). Although the freezing hypothesis was repeatedly rejected for terrestrial birds (e.g. [11]), temperature can be more serious constraint for ectotherms, as supported by the analysis of global amphibian diversity ([47]). In land snails particularly, we need to consider collinearity between the poleward decline in temperature and soil calcium content, likely occurring in most regions due to lower evaporation of soil water and consequent cation leaching at higher latitudes. Content of soil calcium showed a more complex pattern along our latitudinal transect. The amount of calcium dropped steeply between the southern and middle taiga zones, being very low in most of the middle and northern taiga zones (a zone with predominant sandy soils), but increased again in the forest-tundra and tundra zones (Fig. 2A). As land snail species richness typically increases with increasing availability of calcium ([41], [42], [56], [57]), more acidic conditions at higher latitudes can contribute to the decline in species richness independently of temperature. Although the causality of these two factors cannot be disentangled using our data, we suggest that the main effect is that decreasing species richness at higher latitude is primarily determined by low winter temperature, but it is further modified by low calcium levels, which may cause an additional reduction of the number of species. Although extremely calcium-poor conditions occurred in the middle and northern taiga zone due to the predominance of acidic sandy soils, smaller areas of loamy soils can be found there. At 63.5°N we sampled four adjacent forest plots, two on sandy and two on loamy soils. Loamy-soil plots were richer in both the calcium content (ca. 0.51 g/kg) and the number of species (five and three) in contrast to sandy-soil plots with ca. 0.15 g/kg of soil calcium, which hosted only one or no snail species. Higher content of calcium (ca. 1.5 g/kg) in the forest-tundra and tundra soils in comparison with those in the southern taiga zone (ca. 1.3 g/kg) clearly demonstrates that higher calcium content is necessary, but not sufficient condition for achieving a given level of species richness (Fig. 3C). Climatically driven decline in diversity was notable particularly in forests of the forest-tundra zone, which remained very poor in snails even under more calcium-rich conditions (Fig. 2A). The increase in species richness in open habitats of this zone was associated with the first appearance of the arctic *Vertigo* species (Table 1), recorded in wet willow scrub or fen tundra vegetation. These species belong to the smallest land snails, which are able to survive under very low temperature, contrary to the majority of forest species.

The observed responses of land snail species richness to two largely independent factors, water availability and winter temperature, are important for considerations about future changes of latitudinal diversity patterns induced by future climate change ([58]). As geographical patterns of precipitation and temperature shift rather independently, future shifts in the distribution of species and whole ecosystems can be rather complex. This can possibly result in a disintegration of the most suitable zone of the highest diversity, i.e. subtaiga and southern taiga, which are now both warm and wet. Containing nearly 80% of the total snail species number recorded from the steppe to the tundra zone, these two rather narrow zones represent the main diversity hot-spot in this part of northern Eurasia. In this study, we also provided evidence that no single factor is sufficient to explain the unimodal latitudinal gradient in diversity. This adds to a growing body of evidence that multiple factors vary in concert with latitude and interact to cause the latitudinal gradient of species richness both on global and continental scales (e.g. [2], [10], [11], [27], [47], [59]). Our data extend plausibility of this observation also to smaller spatial extents.

**Supporting Information**

**Figure S1** Patterns of selected climatic and environmental variables along the studied latitudinal transect and their pairwise relationships. The upper right part shows values of Spearman correlation coefficient. *(TIF)*

**Figure S2** Changes in land-snail species numbers measured in different habitats and different ways along the studied latitudinal transect and their pairwise relationships. The upper right part shows values of Spearman correlation coefficient. *(TIF)*

**Table S1** Data used in the analyses with numbers of all recorded land snail species (All Sum) at each of the 29 studied sites, mean numbers of species (All Mean), and means of species recorded at open (Open Mean) and forest (Forest Mean) habitats separately at each site; numbers of open and forest plots sampled is given in the second column (Open/Forest). NA refers to the situations where no open or forest habitats were sampled. Values of all explanatory variables used in the study are also provided. *(XLSX)*

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Author Contributions

Conceived and designed the experiments: MC, MH. Analyzed the data: MH. Contributed to the writing of the manuscript: MH, MC.