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Intercontinental dispersal and niche fidelity drive 50 million years of global diversification in *Vertigo* land snails

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Abstract

Aim: We aimed to understand how biogeographical processes and moisture niche ecology contributed to the spatio-temporal diversification dynamics in the land snail genus *Vertigo*.

Location: Global (North America, Europe, Asia, Africa).

Time Period: Cenozoic era.

Major Taxa Studied: Minute terrestrial snails of the genus *Vertigo*.

Methods: We reconstructed a time-calibrated phylogeny of 94 *Vertigo* taxa (~85% of all known extant species) based on mitochondrial and nuclear DNA data. Leveraging this phylogeny with distributional and ecological data from >7000 populations, we performed biogeographic and ecological modelling to investigate evolutionary mechanisms of global *Vertigo* diversification.

Results: *Vertigo* has diversified since the Early Eocene, ca. 47.6 Ma (95% HPD = 46.0–52.7), with its six subgenera originating from the Late Eocene (30.2–48.7 Ma) to the Early Miocene (13.3–23.0 Ma). Species diversity accumulated linearly, with a slight increase 35–30 and 25–20 Ma, coinciding with the emergence of most subgenera and northern hemisphere cooling, respectively. Biogeographic modelling indicated that most diversification events occurred in sympatry (no range modification), but that rare founder events drove global diversification. Soil moisture conditions, a major variable defining *Vertigo* niches, displayed significant phylogenetic signal, but varied less among subgenera relative to within. Shifts in biogeographical ranges and moisture niches (or the absence thereof) were significantly associated at macroevolutionary scales, with most niche shifts upon sympatric cladogenesis and hardly any upon founder-event speciation.

Main Conclusions: Our results indicate that ecological shifts in soil moisture niches occasionally drove cladogenesis in sympatry and anagenetic range extensions, but that long-distance dispersal was mainly successful in the absence of such shifts. A combination of neutral (founder events and drift) and selective mechanisms (adaptive habitat shifts) has determined the macroevolutionary success of *Vertigo*. Our results

Michal Horsák and Bert Van Bocxlaer are equal contributors.

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imply that species with high niche fidelity or fewer opportunities for long-distance dispersal will be more vulnerable to future anthropogenic stressors.

KEYWORDS

biogeographical range estimation, comparative phylogenetics, founder-event speciation, global diversification, moisture niche, Stylommatophora

1 | INTRODUCTION

The recent increase in global distribution data and robust phylogenetic inferences offer new insights into spatio-temporal patterns of biodiversity evolution (Benson et al., 2021; Tobias et al., 2020). Vicariance caused by continental drift, mountain formation, or sea-level fluctuations has been hypothesized to be a principal diversification driver (Carta et al., 2022; Wiley, 1988). However, recent studies also highlighted that long-distance dispersal has contributed to diversification in some taxa (Matzke, 2014; Stelbrink et al., 2020). In addition, shifts in ecological niches and associated adaptation may result in barriers to gene flow among populations, potentially leading to ecological speciation (Marvaldi et al., 2002; Nosil, 2012; Schluter, 2001). At the macroevolutionary level, adaptation to new conditions after arrival may trigger adaptive evolution and radiation (Reznick & Ghahambor, 2001; Chiba, 2002; Ronco et al., 2021; but see Anderson & Weir, 2022). How neutral and selective processes contribute to diversification and what proportion of diversity has resulted from adaptation to contrasting environments (Anderson & Weir, 2022; Van Bocxlaer, 2017), remain unclear for many taxa, especially for invertebrates and taxa capable of long-distance dispersal. Studies on diversification dynamics at large spatial and temporal scales are especially lacking in land snails, because these snails often have spatially restricted distributions (Cameron, 2016; Proios et al., 2021), making it difficult to conduct global analyses across a well-defined clade.

In this context, the diverse genus *Vertigo* provides a unique opportunity to decipher global land snail diversification dynamics. *Vertigo* species have tiny body sizes (shell height varies between 1.2 and 2.7 mm) and commonly reproduce uniparentally (Pokryszko, 1987), both of which enhance their passive dispersal abilities (Nekola et al., 2018). The genus has an excellent fossil record, for example with occurrences in >200 pre-Pleistocene European fossil sites (e.g. Harzhauser & Neubauer, 2021). Because shell features allow placement of several well-preserved fossils reliably in the phylogeny (Nekola et al., 2018), fossil calibration should allow for accurate reconstruction of the tempo of *Vertigo* diversification.

Here, we generated a fossil-calibrated molecular phylogeny including >85% of all known extant *Vertigo* species, and analysed distributional and ecological data from global *Vertigo* population to study how biogeographic processes and ecology have contributed to the spatio-temporal dynamics of *Vertigo* diversification. Given the high passive dispersal capacity and global range of *Vertigo* (Nekola et al., 2018), we hypothesized that founder-event

speciation profoundly shaped *Vertigo* diversification at the macroevolutionary scale. Field data suggest that soil moisture conditions structure *Vertigo* niches (Nekola et al., 2018), as in other land snails (Juříčková et al., 2014), but how stable these niches are over long evolutionary periods is not known, nor whether shifts in moisture niches promoted diversification or how such ecological shifts relate to *Vertigo* range expansion over time. If *Vertigo* species disperse easily, but retain the same ecological niches over long periods, then we expect range expansions to have started early in the diversification history and that closely related *Vertigo* species share similar ecological niches, thus that there is less niche variation within clades than among clades.

2 | METHODS

2.1 | Taxon sampling and DNA markers

We included all 94 species and subspecies of *Vertigo* validated by a recent integrative taxonomic revision representing ~85% of the estimated extant *Vertigo* diversity (Nekola et al., 2018). For each of these taxa, we compiled distribution and ecological data from >7000 populations worldwide, allowing for documentation of intraspecific ecological variation. Geographical ranges of the species vary from very restricted (i.e. only 16 km² for *V. cupressicola*) to almost the entire northern Holarctic (*V. ronneyensis*), with most species having sub-continental distributions. Additional information on the distribution and ecology of *Vertigo* species can be found in Nekola et al. (2018). As our aim is to study diversification processes without interference from intraspecific coalescent processes, phylogenetic analyses were conducted with a single representative specimen per species or subspecies. These specimens were selected based on completeness of the molecular data and taxonomic considerations from a larger dataset with 429 individuals that included representatives from various distant populations per species to cover intraspecific genetic diversity (see Nekola et al., 2018). Many of our nucleotide sequences were already available, but some were newly generated (Table S1 in Appendix S1; see also Appendix S2 for single loci matrices). We used *Nesopupa* sp., the sister genus of *Vertigo*, as outgroup (Nekola et al., 2023). Our molecular data consisted of two mitochondrial and two nuclear DNA markers, namely cytochrome b (CYTB), 16S ribosomal RNA (16S rRNA), and Internal Transcribed Spacers 1 and 2 (after concatenation referred to as ITS), respectively. Primer sequences are provided in Table S2 in Appendix S1; for details on

gene fragments and sequence alignment see Appendix S1, M1. Each *Vertigo* taxon was represented across all four loci (there was no missing data for ingroup taxa).

2.2 | Phylogenetic inference and assessment of mitonuclear discordance

Maximum likelihood trees were obtained in IQTREE 2.2.0 (Minh et al., 2020), using two partitions for the nuclear matrix (ITS, and ITS-gaps) and four partitions for the mitochondrial matrix (CYTB-1st+2nd codon position, CYTB-3rd codon position, 16S rRNA, and 16S rRNA-gaps). The best partitioning scheme and best-fit models of substitution for each partition were determined by IQTREE through MODELFINDER (Kalyaanamoorthy et al., 2017). Branch support was obtained through 10,000 replicates of ultrafast bootstrap (Hoang et al., 2018), and values ≥ 95 were considered highly supported.

Because gene tree/species tree discordance is common at shallow phylogenetic levels (Maddison, 1997), we first conducted separate phylogenetic analyses of the mitochondrial and nuclear loci. As we did not find evidence for mitonuclear discordance in the deeper splits of *Vertigo*, that is, those reflecting subgenus relationships and directly descending diversification events, with an approximately unbiased test (see Appendix S1, M1; Figure S1 in Appendix S1, and Appendix S2 for AU test), mitochondrial and nuclear data were combined for downstream analyses to maximize support across various scales of divergence. Cases of mitonuclear discordance along shallow branches (Figure S1 in Appendix S1) could result in topological uncertainty and low support in combined analyses. The final IQTREE analysis was conducted with the same configuration per fragment as in independent gene tree analyses (see Appendix S2 for all IQTREE results).

2.3 | Divergence time estimation

Divergence time estimation was conducted in BEAST 1.10.4 (Drummond et al., 2012), with a Yule or birth-death speciation process as tree prior, and with the upper age bound on the split between *Vertigo* and *Nesopupa* as 87 or 130 Ma (see below), resulting in four analyses in total. For each analysis, four independent chains were run, each for 50 million generations, sampling every 2500, and discarding the first 25% generations as *burn-in*. Convergence between replicate runs and the effective sample size (>300) on parameter values were assessed with TRACER 1.7 (Rambaut et al., 2018). Lognormal (uncorrelated) relaxed clocks were defined for each partition. Topological constraints (see Figure S2 and M1 in Appendix S1) were applied to all clades recovered with high support in the concatenated ML analysis to reduce the tree space that was to be explored by BEAST and to increase the precision of the divergence time estimation.

Two scenarios for the upper age bound on the split between *Vertigo* and *Nesopupa* were implemented based on phylogenetic analyses of Panpulmonata with genome-wide data (Teasdale, 2017).

No representatives of Vertiginidae (to which *Nesopupa* and *Vertigo* belong) were included by Teasdale (2017), but the family belongs to Orthurethra (Nekola et al., 2023; Saadi et al., 2021) and the most basal divergence within Orthurethra was reconstructed to ~85 Ma (implemented as 87 Ma to account for uncertainty), whereas the age of the MRCA of Orthurethra and the divergent Clausilioidea was ~130 Ma. Therefore, we used 87 and 130 Ma, respectively, to constrain the maximum age of the split between *Vertigo* and *Nesopupa*. We further constrained the timing of divergence within *Vertigo* with seven reliably dated fossil calibration points that are unambiguously placed in the phylogeny (branches with high support), covering both deep and shallow divergences (Table S3 and M2 in Appendix S1). For each calibration point, we set uniform priors with the minimum age estimate of each fossil as the lowest bound for the clade that they define in the *Vertigo* phylogeny, whereas the maximum age was conservatively set to the upper bound of the split between *Vertigo* and *Nesopupa* (87 or 130 Ma, respectively). Because the age of *Vertigo* and its branching pattern were very similar regardless of the tree prior and the upper bound for the split between *Vertigo* and *Nesopupa* (Appendix S2), we used the tree generated with the simpler Yule prior and the more probable 87 Ma maximum age bound for downstream analyses (see Appendix S2). The outgroup *Nesopupa* sp. was removed for these downstream analyses.

2.4 | Analysis of diversification dynamics

The study of how biogeographic processes and ecology have contributed to the spatio-temporal dynamics of *Vertigo* diversification requires examining whether major shifts in diversification rates occurred along the phylogeny, and if so, whether such shifts relate to changes in ecology or biogeographical ranges. First, we performed lineage-through-time plots by randomly sampling 1000 trees from the posterior distribution of BEAST trees using APE v.5.6-2 (Paradis & Schliep, 2019) in R v.3.6.1 (R Core Team, 2019). Diversification patterns were compared with the 95% confidence intervals (CI) on pure birth and birth-death models parameterized from the empirical data using PHYTOOLS v.0.6-99 (Revell, 2012). We then examined whether shifts in diversification rates occurred along the *Vertigo* phylogeny with a Bayesian analysis of macroevolutionary mixtures using BAMM v. 2.5.0 (Rabosky et al., 2013). Priors for speciation and extinction rates were defined using setBAMMpriors of BAMMTOOLS v. 2.1.6. (Rabosky et al., 2014). We conducted the analyses with 10 million MCMC generations, sampling every 10,000 generations, with a burn-in of 10%. We performed three independent runs, and verified convergence by comparison of log-likelihoods over the MCMC and by calculating effective sample sizes in CODA v.0.19-3 (Plummer et al., 2006). The sampling fraction was conservatively defined as 80%, which was obtained considering the 94 included (sub) species for a total known diversity of ~110 species, supplemented with seven species that are yet to be discovered or taxonomically reassigned to *Vertigo*, including Australian *Cylindrovertilla* species (see Figure 1). We also examined whether diversification in *Vertigo*

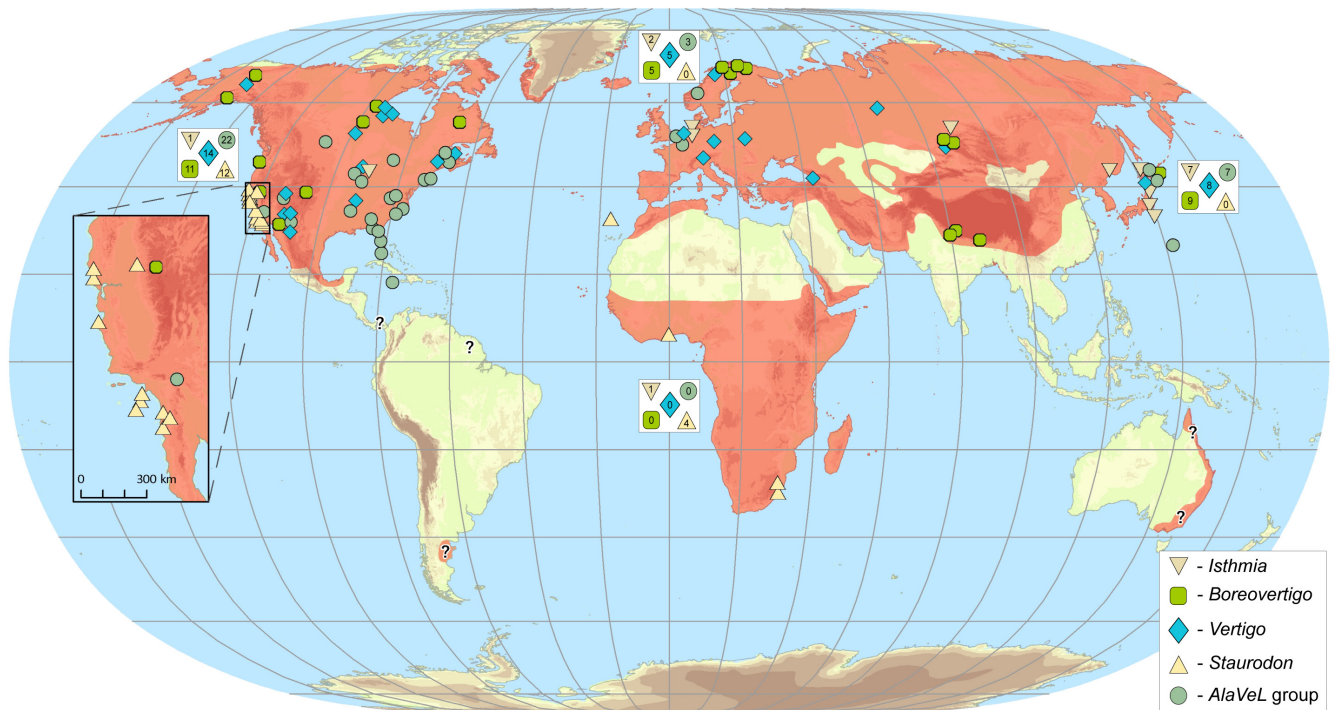


FIGURE 1 Map showing the known distribution of *Vertigo* (with minor extrapolations) as red polygons. Symbols indicate the location of all samples used in the phylogenetic analyses (see Figure 2). Panels of larger symbols in insets indicate the number of *Vertigo* species per subgenus at each continent. Question marks depict areas of distribution where *Vertigo* has never been reported, but that are occupied by taxa which likely belong to *Vertigo*.

was diversity-dependent or independent with the R package DDD v.4.1 (Etienne & Haegeman, 2019). We calculated the log-likelihood of both models and compared them with a corrected Akaike Information Criterion (AICc).

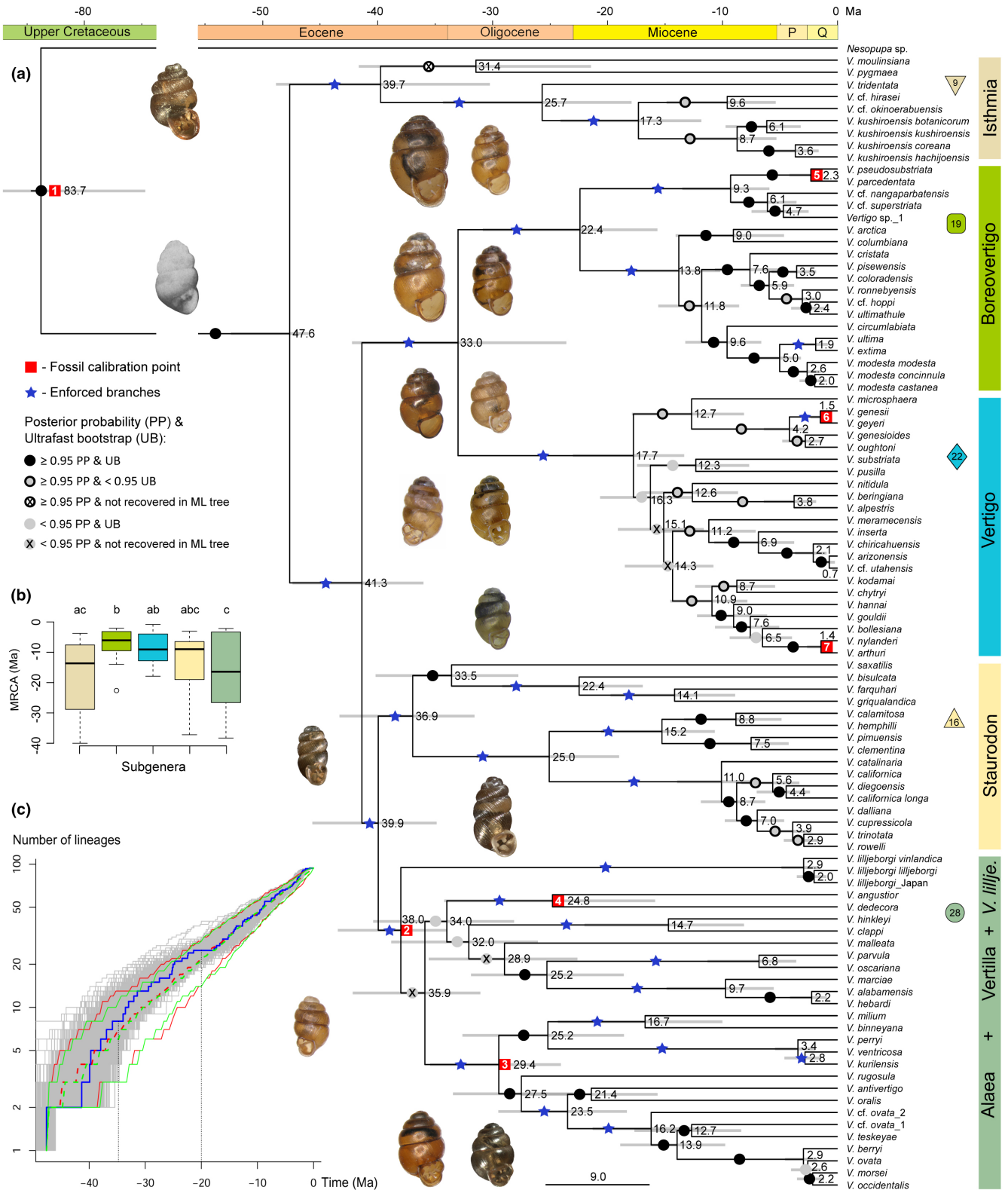
2.5 | Biogeographical analysis

We estimated ancestral ranges with a phylogenetic approach to biogeography using six reticulate models, as implemented in BioGeoBEARS v.1.1.2: DEC, DIVALIKE, and BayAreaLIKE, fitted either with or without the parameter J (Matzke, 2014, 2018, 2022), accounting for jump-dispersal at cladogenesis, therewith, integrating founder-event speciation. Model fitness among these six models was compared using AICc.

Vertigo is confirmed from four continents (North America, Europe, Asia and Africa; Figure 1) which were analysed as distributional units without further subdivision, as we intended to understand global biogeographical patterns. Species distribution data are presented in Table S1 in Appendix S1. Although Europe and Asia form a single land mass, we considered them separate due to consistent differences in climatic niche models for land snail species (see Nekola et al., 2022). Non-native occurrences, for example, the recent anthropogenic introductions of *Vertigo pygmaea* in North America, were not considered when coding geographic ranges.

Biogeographic analyses were performed with the maximum clade credibility (MCC) tree reconstructed with BEAST. As the topology of this phylogeny was not fully resolved in certain subclades, we examined the robustness of our biogeographic model comparisons and ancestral range estimations under topological uncertainty (see

FIGURE 2 (a) *Vertigo* phylogeny based on the concatenated dataset of mitochondrial (16S rRNA and COI) and nuclear (ITS1 and ITS2) markers. Branch supports from Maximum Likelihood (IQTREE) and Bayesian time-calibrated (BEAST) analyses are summarized on the BEAST tree. Values and bars on nodes represent mean node ages and 95% confidence intervals, respectively. Fossil calibration points are numbered as in Table S2 in Appendix S1. Subgenus symbols are as in Figure 1, with an indication of the number of taxa in each subgenus. Shell images represent the outgroup (*Nesopupa* sp.), the oldest known *Vertigo* shell (image adopted from Good, 1987), and the extant species (from left to right, top to bottom): *Vertigo moulinsiana*, *V. kushiorensis botanicorum*, *V. arctica*, *V. parcedentata*, *V. genesii*, *V. substriata*, *V. pusilla*, *V. chytrij*, *V. nylanderii*, *V. californica longa*, *V. calamitosa*, *V. angustior*, *V. antivertigo*, *V. ventricosa*. Shell height varies from 1.7 to 2.5 mm. (b) Variation in mean time estimates of MRCAs for all splits within subgenera; small letters indicate significant differences based on a Kruskal–Wallis test ($p=0.025$) with post-hoc pairwise Dunn's tests. (c) Cumulative number of lineages over time for 1000 trees subsampled from the BEAST posterior (grey lines), as well as for the BEAST MCC tree (blue line) compared with the mean expectations and 95% CIs under a pure birth (red) and birth-death model (green). Two vertical grey lines delimit the period with a slightly elevated number of diversification events.



Appendix S1). Specifically, we collapsed all uncertain branches and randomly resolved them after which we performed biogeographic analyses with a sample of the randomly resolved phylogenies.

We examined the role of anagenetic (dispersal, extinction) and cladogenetic biogeographic processes (sympatric divergence, subset sympatry, vicariance, and jump-dispersal) in shaping the distribution

of *Vertigo* via biogeographical stochastic mapping (BSM; Dupin et al., 2017). This analysis was performed in BioGeoBEARS with 1000 replicates and using the parameters of the best-fit biogeographic model as priors. The support for competing processes was compiled over the 1000 replicates. In certain cases, several underlying processes could explain the observed patterns. If a process received over

80% support, we considered it dominant, but alternatively, a combination of the two most supported processes was required to reach 80% support, in which case we reported the dominant process followed by the secondary process to describe biogeographic patterns.

2.6 | Analyses of moisture niche evolution

Soil humidity conditions set important constraints on *Vertigo* niches, which translate to the species occurrences (e.g. Nekola et al., 2018; Speight et al., 2003). Although moisture niches are defined along a continuous gradient, for practical reasons, we covered this gradient with three categories: xeric, mesic or wetland. Moisture niches were thus assigned based on the habitat characteristics of *Vertigo* species (Table S1 in Appendix S1). Some *Vertigo* species display intraspecific moisture niche variability and commonly occur in more than a single moisture type. Therefore, these were classified as xeric/mesic, mesic/wetland or xeric/mesic/wetland, resulting in six types of moisture niches.

We estimated ancestral moisture niches as a multistate discrete character with six states using three transition models, equal rate, symmetric rate or all rates different, and joint reconstruction as implemented in APE, and also tested for phylogenetic signal with PHYTOOLS. Secondly, because our primary goal was to examine whether changes in moisture niches are associated with alterations of biogeographic ranges or the absence thereof, we also adopted the same analytical framework as for the biogeographical analyses but with an eco-matrix coding moisture niches, rather than geographical ranges, resulting in an estimation of moisture niches as a three-state character (xeric, mesic, wetland) allowing intraspecific moisture niche variability (xeric/mesic, mesic/wetland or xeric/mesic/wetland).

Finally, we examined whether an association existed between shifts in biogeographic ranges and moisture niches, by coding along which branches range and niche shifts occurred (0=no shift; 1=shift). Subsequently, we evaluated whether shifts in biogeography and in ecology are significantly related using a χ^2 -test with contingency correction, and more specifically, whether ecological changes along branches or upon diversification are linked to specific biogeographic processes, again with χ^2 -tests.

3 | RESULTS

3.1 | Phylogenetic reconstruction

Overall, our *Vertigo* phylogeny is well-resolved and highly supported (Figure 2a). In total, 83 of 94 branches (88%) were highly supported in the BEAST phylogeny (Figure 2), 68 of which were also highly supported in the IQTREE analysis (Figure S2 in Appendix S1). Only 11 branches (12%) lacked good support in both the IQTREE and BEAST analyses. Deeper nodes and five of the six major clades of *Vertigo*, traditionally considered subgenera, were highly supported. The subgenus *Isthmia* was strongly recovered as sister to the other subgenera, which were grouped into two major clades: *Vertigo*+*Boreovertigo*, and *Staurodon*

+ (*Alaea*+*Vertilla*+*V. lilljeborgi*; i.e., the *AlaVeL* group). The basal nodes of the subgenus *Vertilla* and its relationships within the *AlaVeL* group remained unresolved. Finally, at shallower levels, some nodes, mostly within the subgenera *Isthmia* and *Vertigo*, were incompletely resolved, in part due to mitonuclear discordance (see Figure S1 in Appendix S1).

3.2 | Divergence time estimates and diversification rates

Our time-calibrated phylogeny indicates that the diversification within *Vertigo* began in the Early Eocene, ca. 47.6 Ma (95% HPD=46.0–52.7), by the split between the subgenus *Isthmia* and the rest of *Vertigo*. Time estimates for the MRCAs of *Vertigo* subgenera differed widely from the Late Eocene to Early Miocene (Figure 2a): *Isthmia* (mean time estimate=39.7 Ma; 95% HPD=30.2–48.7); *Staurodon* (36.9 Ma; 31.5–43.3); the *AlaVeL* group (38.0 Ma; 33.9–43.4); *Alaea* (29.4 Ma; 24.0–35.4); *Boreovertigo* (22.4 Ma; 15.6–30.8) and *Vertigo* (17.7 Ma; 13.3–23.0).

There was a steady accumulation of lineages through time, with a slightly elevated number of lineages in the period 35–20 Ma ago compared with average expectations under pure birth and birth-death models, but this increase remains within the 95% CI for these models (Figure 2c). The timing of within-subgenus diversification differed substantially among subgenera, as demonstrated by significant differences in the divergence times for species-level splits (Figure 2b; Kruskal-Wallis test=0.025): Species-level divergences within subgenera *Boreovertigo* and *Vertigo* were significantly younger than those within the *AlaVeL* group (Dunn test, $p < 0.038$), and those of *Boreovertigo* were also significantly younger than those of *Isthmia* ($p < 0.023$).

Our BAMM analyses all converged (ESS values were >700) towards the same result, namely that no major shifts in diversification rates occurred between clades or at any particular time in the phylogeny (Figure S3 in Appendix S1). However, speciation rates gradually decreased over time, whereas extinction rates were reconstructed as very low and constant, so that net diversification rates also gradually decreased over time. The actual number of observed *Vertigo* species is substantially below the expected number of ~220 species under the assumption of a diversity-dependent model, but model comparisons provided strong support for diversity-independent diversification (AICc weight 88.77%).

3.3 | Biogeographical range evolution

Out of the six models of range evolution (Table 1), DEC+J received the strongest support (AICc weight: 0.74), but DIVALIKE+J also received considerable support (AICc weight: 0.23). Both DEC+J and DIVALIKE+J yielded very similar parameter estimates, resulting in equivalent biological conclusions. Models consistently received much higher support when implemented with parameter +J than without it, indicating that founder-event diversification contributed strongly to range alterations in *Vertigo*. Highly similar results

TABLE 1 Results of fitting six reticulated models of *Vertigo* range evolution to our BEAST MCC phylogeny.

Model	LnL	#pars	d	e	j	AICc	AICc_wt
DEC	-141.2	2	0.008	<0.001	n.a.	286.6	<0.001
DEC+J	-132.7	3	0.005	<<0.001	0.026	271.7	0.740
DIVALIKE	-140.3	2	0.008	<<0.001	n.a.	284.7	0.001
DIVALIKE+J	-133.9	3	0.006	<<0.001	0.022	274.0	0.230
BAYAREALIKE	-177.9	2	0.006	0.027	n.a.	360.0	<<0.001
BAYAREALIKE+J	-136.2	3	0.004	<<0.001	0.039	278.7	0.023

Note: Model-fit is evaluated with a corrected Akaike information criterion and its associated weight.

Abbreviations: #pars, number of parameters; d, dispersal; e, extinction; j, jump-dispersal; LnL, Log-likelihood (base e).

were consistently retrieved upon collapsing and randomly resolving weakly supported branches in the BEAST phylogeny and refitting the biogeographical models, implying that these results are robust to uncertainty caused by mitonuclear discordance (Table S4 and Figure S4a–e in Appendix S1). Throughout all of these analyses, the extinction parameter was low, which is consistent with our BAMM results, and the similarities in the accumulation of lineages through time under pure-birth and birth-death models in *Vertigo*.

BSM indicated that most distributional range changes occurred upon cladogenesis, with only 16 out of 187 branches showing anagenetic dispersal (Figure 3). Most cladogenetic events occurred in sympatry (parameter γ ; 73 nodes of 93), followed by jump-dispersal (parameter j ; 11). Subset sympatry (parameter s) and vicariance (parameter v) were estimated as less common (6 and 3 nodes, respectively).

Although the majority of *Vertigo* diversity is known from North America (60 of 94 taxa), *Vertigo* may have originated in either North America or Eurasia (Figure 3). *Isthmia* is the only subgenus with an estimated origin in Asia, where most of its species still occur, although the subgenus is distributed across all four continents. All other subgenera have their estimated origin in North America and currently occur on two to three continents. The subgenera *Boreovertingo* and *Vertigo* show a slight dominance (ca. 60%) of species that occur in North America, whereas the subgenus *Staurodon* and the *AlaVeL* group have proportionally more North American species ($\geq 75\%$). *Staurodon* contains two main clades, however, which are reciprocally restricted to Africa and North America.

Our results indicate that long-distance dispersal occurred repeatedly across all subgenera of *Vertigo* and at all moments throughout the diversification history, from almost at the subgenus level, for example, the colonization of Africa from North America in *Staurodon*, down to sister species splits, for example, the colonization of Asia from North America by the ancestors of *Vertigo kurilensis*. Intercontinental dispersal occurred mainly from North America to other continents, except in the subgenus *Isthmia*, which colonized North America secondarily and in the subgenus *Vertigo*, where repeated range shifts involving North America, Asia, and Europe were reconstructed.

3.4 | Moisture niche evolution

We found significant phylogenetic signal in the moisture niches of *Vertigo* species (Blomberg's $K=0.559$, $p=0.001$; Pagel's $\lambda=0.826$,

$p<0.001$). Reconstructing ancestral moisture niches as a six-state discrete character resulted in strong support for a model with a symmetric niche transition matrix (AIC weight=99.76%). This transition matrix indicated high fidelity of *Vertigo* species to moisture niches, with rare transitions occurring mainly between xeric and xeric/mesic habitats or much less frequently between mesic, mesic/wetland and wetland habitats, thus four out of 15 possible (symmetric) transition types (Figure 4b). The ancestral niche for the MRCA of *Vertigo* was most likely mesic (91.3%), although wetland (5.5%) or mesic/wetland (2.8%) conditions received some support too (Figure 4a).

Ecological modelling of moisture niches with a three-state matrix and intraspecific polymorphism along the *Vertigo* phylogeny revealed results congruent with the above-mentioned approach but states that resemble those under marginal (rather than joint) ancestral state estimation (Figure S5 in Appendix S1). Under this estimation, the MRCA of *Vertigo* most likely occurred in mesic/wetland, mesic or xeric/mesic/wetland conditions. Subgenus clades of *Vertigo* are typically estimated to have occupied a mixture of mesic and wetland conditions, apart from the subgenus *Staurodon*, which would have occupied a mixture of xeric and mesic niches. With the exception of *Staurodon*, we typically found the same range of moisture niches within each subgenus; however, usually the various states were not randomly distributed among taxa within subgenus clades. Indeed, clades of related species usually share similar moisture niches (species-level splits). For example, within the *AlaVeL* group, *Alaea* was estimated to be composed almost entirely of species associated with very wet, mostly swampy habitats, which was likewise the case for the *V. lilljeborgi* subclade. However, the subgenus *Vertilla* was inferred to occupy mesic rather than wetland environments. Similarly, the majority of species in the subgenus *Vertigo* was estimated to only have inhabited mesic habitats, except for the most basally divergent subclade including the *V. genesii* group, which almost exclusively comprised species that were estimated to have occupied wetland habitats.

3.5 | Eco-evolutionary link of range and niche evolution

Upon comparing shifts in biogeographical ranges and moisture niches, we found patterns that significantly deviate from random,

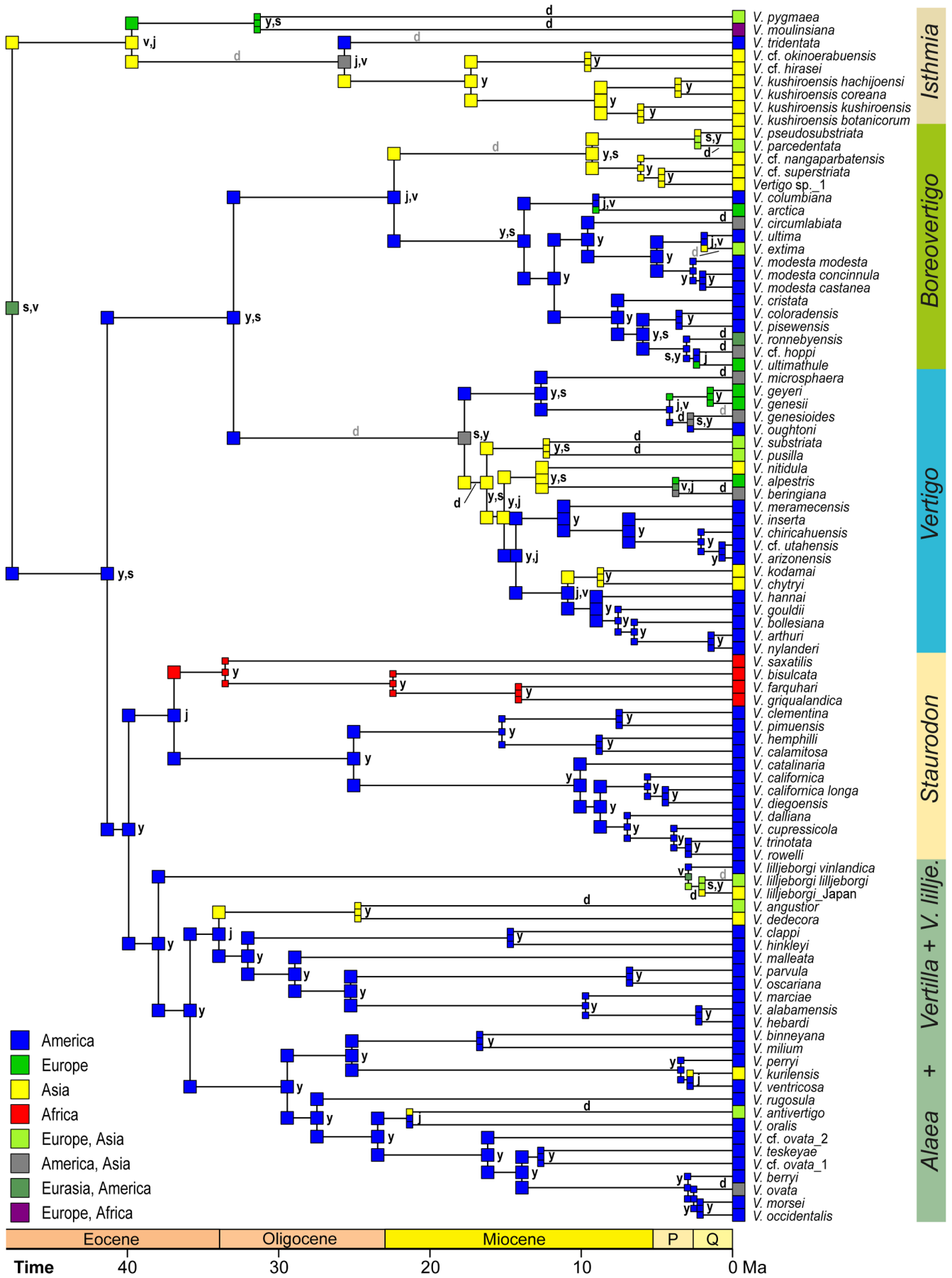


FIGURE 3 *Vertigo* species-level phylogeny with ancestral range estimations obtained from fitting the DEC+J model; biogeographic processes were inferred from Bayesian stochastic mapping (BSM) with 1000 iterations. If one biogeographic process is presented at a node, it received >80% support in BSM, whereas if two processes are mentioned, the first received most support, with the joint support for both being usually >80% (and in all cases >69%). Anagenetic dispersal is represented in greyscale if it was the non-dominant process, but required to jointly reach >80% support. d, anagenetic dispersal; j, jump-dispersal; s, subset sympatry; v, vicariance; y, sympatry.

indicating an association between changes in both ($\chi^2=5.05$, $p=0.025$). Of 186 branches, 121 had no change in biogeographic range nor moisture niche, whereas in 14 cases changes in both coincided. Changes involving only biogeographic range (27 cases) or only moisture requirements (24 cases) were equally common. We also observed high stability in the moisture niche when cladogenesis was associated with jump-dispersal ($\chi^2=7.36$, $p=0.007$) and sympatry ($\chi^2=13.16$, $p<0.001$; Table 2), although changes in moisture niches upon diversification in sympatry were proportionally more common. The other biogeographic processes did not show a significant association with moisture habitats (Table 2), but at least vicariance and subset sympatry were not sufficiently common to make conclusions.

4 | DISCUSSION

Phylogenetic inference from four concatenated markers allowed us to unambiguously reconstruct the relationships between the vast majority of extant *Vertigo* species and clades. Fossil calibration of divergence times further provided robust temporal constraints to study *Vertigo* diversification in biogeographic and ecological contexts. Previous phylogenetic work on terrestrial gastropods has either been limited to smaller spatial scales (e.g. Brozzo et al., 2020; Neiber et al., 2022; Razkin et al., 2015) or featured less comprehensive sampling of included clades (e.g. de Weerd & Gittenberger, 2013; Saadi et al., 2021; Teasdale, 2017; Wade et al., 2006). In this context, our analysis of *Vertigo* diversification dynamics provides a unique opportunity to understand eco-evolutionary drivers of land snail diversification at large spatio-temporal scales.

4.1 | Time-calibrated phylogenetics reveal steady diversification with an early onset

The diversification in *Vertigo* started early compared with that of other land snail genera. The onset of diversification of snail clades considered to represent individual genera typically occurred in the last 20Ma in Clausilidae, Helicidae and Hygromiidae, but since 28.6Ma in *Oxychilus* (Neiber et al., 2022), all of which are young compared with the onset of diversification in *Vertigo* ~50Ma. *Vertigo* species accumulated steadily over time and across subgenera, with a decrease in net diversification towards the present, which is not indicative of diversity-dependent diversification, however. BAMM and biogeographic range estimations congruently indicated low extinction rates in *Vertigo*, which resulted in high similarity in pure birth and birth-death analyses. Considering methodological difficulties in

estimating extinction rates from time-calibrated phylogenies of extant taxa alone (Louca & Pennell, 2021; Morlon et al., 2011), and independent knowledge on the *Vertigo* fossil record, comprising 45 described extinct species, the inferred low extinction rates likely represent an artefact.

4.2 | Climate cooling as a driver of *Vertigo* diversification

Although *Vertigo* lineages accumulated steadily through time, we observed a slight increase in diversification 35–30Ma, related to the evolution of several subgenera, and 25–20Ma, that is, around the Oligocene–Miocene transition (~23Ma). Whereas global temperatures were reconstructed to be warm in the Late Oligocene, Early Miocene temperatures would have displayed large-scale fluctuations leading afterwards to generally cooler and dryer terrestrial ecosystems (Beddow et al., 2016; Steinthorsdottir et al., 2021). During the Miocene cooling at high and mid-latitudes, which resulted in dramatic changes in floras (Steinthorsdottir et al., 2021), the subgenera *Boreovertigo* and *Vertigo* started to diversify. This period also coincided with extensive tectonic activity and uplift of the Himalayan plateau (Spicer et al., 2021), where one of the basal clades of *Boreovertigo* primarily occurs, suggesting that it diversified there as this plateau formed. Thus, global climate change at mid- and high latitudes may have played a causal role in this increased lineage diversification in *Vertigo* around the Oligocene–Miocene transition, but the later, Pleistocene diversification dynamics of *Vertigo* also seem to be paced by glacial–interglacial climate cycles (Stewart et al., 2010). We found 13 splits with a mean reconstructed age of less than 2.6Ma, resulting in 23 taxa (16 of which are considered species). Most of these were observed in the subgenera *Boreovertigo* and *Vertigo*, consisting largely of species restricted to temperate and boreal climates. These subgenera may present an interesting study system for further population-level analyses in the context of glacial–interglacial cycles.

4.3 | Jump-dispersal shapes distributional patterns

Diversification in *Vertigo* mainly occurred in geographic sympatry, at least at continental scales, but intercontinental jump-dispersal occurred several times, mainly from North America to other continents. However, because the subgenera *Isthmia* (*V. tridentata*) has secondarily colonized North America, it seems that all biogeographic regions may act as sources for new colonization events.

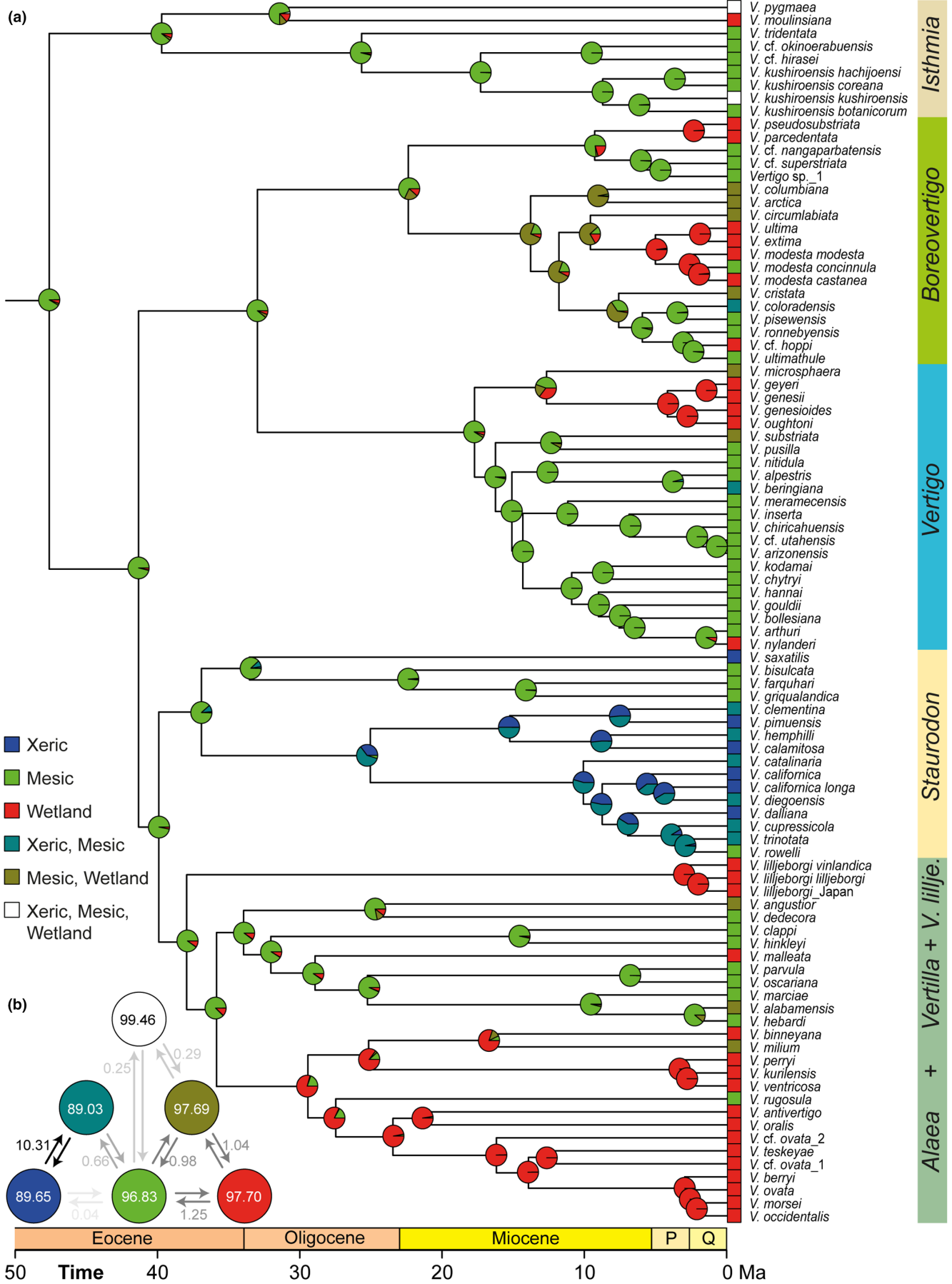


FIGURE 4 (a) Estimation of ancestral moisture-related ecological niches along the *Vertigo* phylogeny with a six-state discrete character using the best-fit symmetric transition model. (b) Graphical representation of the moisture niche transition matrix. Transition frequencies are indicated with greyscale arrows (the darker the more frequent), illustrating that only 4 out of 15 possible transition types are regularly observed.

TABLE 2 Association between ecological changes in moisture niches and range alterations.

	Vicariance	Jump-dispersal	Sympatry	Subset sympatry	Anagenetic dispersal
Stable	1	10	52	5	8
Modified	2	1	21	1	8
Significance	0.564	0.007	<0.001	0.103	1.000

Note: Moisture niches are either stable or modified upon range modifications associated with four cladogenetic processes (vicariance, jump-dispersal, sympatry, and subset sympatry) and anagenetic dispersal. Note that only dominant biogeographical processes were considered to avoid pseudoreplication. Differences were tested by χ^2 -tests under the assumption of random distribution. Significant results are in bold; the cut-off level after Bonferroni correction was $\alpha = 0.01$.

Such founder events have occurred at various times throughout the evolutionary history of *Vertigo*, impacting individual extant species, such as *V. antivertigo* and *V. kurilensis*, but older colonizations have also led to new clades, such as the African clade in the subgenus *Staurodon* or the Himalayan clade in *Boreovertigo*. This result contrasts with, for example, Viviparidae, for which founder events were also inferred, but only for deeper splits in the phylogeny (Stelbrink et al., 2020). The high capacity of long-distance dispersal and regular establishment in new regions may explain the diversity-independent nature of *Vertigo* diversification, which we had not expected as several *Vertigo* species regularly co-exist, with up to five species per site (Nekola et al., 2018).

Zoochory by migratory birds is a plausible mechanism for intercontinental dispersal, which is well-documented in the cauliid genus *Balea* that repeatedly colonized highly remote oceanic islands (Gittenberger et al., 2006). Previous studies of land and freshwater snails considered transoceanic dispersal to be very rare. They explained intercontinental distributions primarily via the disruption of larger land masses by continental drift, implying a more dominant role for vicariance (Herbert & Mitchell, 2008; Wade et al., 2006). Very few cases of vicariance were inferred for *Vertigo*, and only once as the sole inferred process, namely, the (most likely Pleistocene) segregation of three geographically isolated subspecies within the Holarctic *V. lilljeborgi* clade. Climate modelling indicates that these three subspecies occupy highly disjunct regions, separated by vast areas with unfavourable climate (Nekola et al., 2022). Although we did not find that vicariance is a main driver of diversification in *Vertigo* at the continental scale (as most continents separated prior to the origin of *Vertigo*), it still may operate at subcontinental scales, which requires further in-depth study.

4.4 | Moisture niches are conserved, with rare shifts over geological time

How ecology contributes to diversification, and whether diversification is promoted by niche conservatism versus ecological

versatility has been extensively debated, with empirical examples providing evidence for both hypotheses (Marvaldi et al., 2002; Nosil, 2012; Wiens & Graham, 2005). Niche conservatism may limit adaptation to conditions at geographic boundaries, and therewith, affect allopatric speciation (Wiens, 2004). However, in the case of frequent long-distance dispersal, niche versatility and large adaptive capabilities may be instrumental in allowing establishment and subsequent evolution in new environments. Soil moisture niches display significant phylogenetic signal in *Vertigo*, but vary more within *Vertigo* subclades than among them, indicating that habitats with different moisture conditions have been colonized rarely but repeatedly over the course of 50 Ma. Estimations of moisture niches along the phylogeny with various methods resulted in similar, robust results, with most *Vertigo* subgenera sharing mesic and wetland conditions, although one type of condition usually dominates over the other per subgenus. Xeric environments have been colonized less frequently, with *Staurodon* as a notable exception, which is the only subgenus that has successfully colonized and diversified in sub-Saharan Africa. These results indicate that *Vertigo* displays overall niche conservatism and that versatility as to moisture niches is rare, but that it has occasionally driven diversification.

4.5 | Shifts in geographic ranges and niches are associated with *Vertigo* diversification

Shifts (or the absence thereof) in biogeographic ranges and moisture niches were significantly associated at global and macroevolutionary scales. Both ranges and niches typically remain stable upon diversification, including during founder events and sympatric cladogenesis, however diversification in sympatry was more frequently associated with shifts in moisture niches (21 out of 73 cases) than in founder-event diversification (1 out of 11 cases). Changes in moisture niche were commonly associated with anagenetic dispersal (8 out of 16 cases), suggesting that ecological versatility may have promoted dispersal into new areas. From these results, we can conclude that some *Vertigo* clades and species display flexibility as to moisture niches, but

that shifts in moisture niches have rarely driven diversification and range extensions. The success of long-distance dispersal in *Vertigo* is substantially enhanced if moisture conditions are similar in the source region and the invaded range. Although our analyses focused on moisture niches, other ecological variables may have contributed to differential adaptation and speciation, and patterns of regular co-occurrence among several *Vertigo* species merit further eco-evolutionary study.

In summary, our results indicate that both neutral mechanisms, such as founder-event speciation and drift, and selective mechanisms, such as differential adaptation upon ecological niche shifts, have contributed to divergence and the evolutionary success of *Vertigo*. Whereas global ecological changes and shifts in niche preferences have occasionally promoted range shifts and diversification, such events are not the main feature of *Vertigo* diversification. The ability to disperse passively over long distances and conservatism of moisture niches upon such dispersal have strongly influenced macro-evolutionary diversification dynamics of *Vertigo*. These trajectories are determined by the patchy and often sympatric occurrence of different *Vertigo* species and the spatio-temporal dynamics by which suitable habitats emerge and disappear across the landscape (Horsák et al., 2012). In this context, increasing habitat destruction and fragmentation by humans, along with increasing climate variability due to climate change, is likely to accelerate the rate at which habitat patches become temporarily unsuitable. Such disturbance may have a particular impact on *Vertigo* species, especially those with lower dispersal capacity and those that occur in areas where habitats with favourable conditions are more patchy and/or more difficult to access.

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

All data underlying this article are provided in the Supplementary Information.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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