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First evidence for long-term stasis in wet-tropics land snail community composition

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While spatial turnover in species composition is well documented (Whittaker 1975, Condit et al. 2002) much less investigation has been conducted over long-time periods. Land snails provide a unique window to observe such patterns because their fossil shells not only allow for species-level identifications and quantification of abundance (Schilthuizen 2011), but can also provide accurate radioisotope dates (Pigati et al. 2010). Here we compare species turnover and accumulation patterns in comparable temperate (Slovakia and the Czech Republic) and tropical (Malaysian Borneo) land snail datasets. These analyses show that while temperate communities demonstrated significant compositional change over the modern to Late glacial maximum (LGM) transition, tropical communities did not.

Dissimilarity in both datasets was driven by species turnover (0.74 versus 0.65 for temperate versus tropics) rather than by differences in richness (0.13 versus 0.07). Highly significant temporal distance decay (DD) in species composition was noted (Fig. 1) for the temperate dataset ($p \ll 0.0001$) while no significant decay was noted over the same period in the tropics ($p = 0.28$). Thus while over 70% of observed similarity decay was explained by temporal distance in Slovakia/Czech Republic, less than 10% was explained in Malaysia. AICc value comparison in the temperate data indicated that a two-parameter exponential form (-44.1) was much better fit to the data than a two-parameter power-law form (-25.6). Important differences were also noted in the shape of the species–time relationship (STR). While Slovakia/Czech Republic data demonstrate a 78% cumulative increase of species over the modern–LGM axis, the Malaysian data accumulated a dozen fewer species over the same temporal extent. The tropical data also exhibited a more pronounced asymptote: while cumulative temperate species richness demonstrated a 50% increase in cumulative richness from 0.3–25 ka, tropical richness only increased 20% over the same period.

These analyses demonstrate that while there has been continual turnover in land snail assemblages in the temperate system, the tropical system demonstrated compositional stasis. Observed turnover in the temperate system was expected given regional biome change from the cold and dry LGM to wet and warm modern. Such directional change in the regional species pool is supported by extensive fossil evidence (Ložek 1964) and is further documented by the exponential form of the temporal DD relationship (Nekola and McGill 2014). At least some turnover was expected from the Malaysian

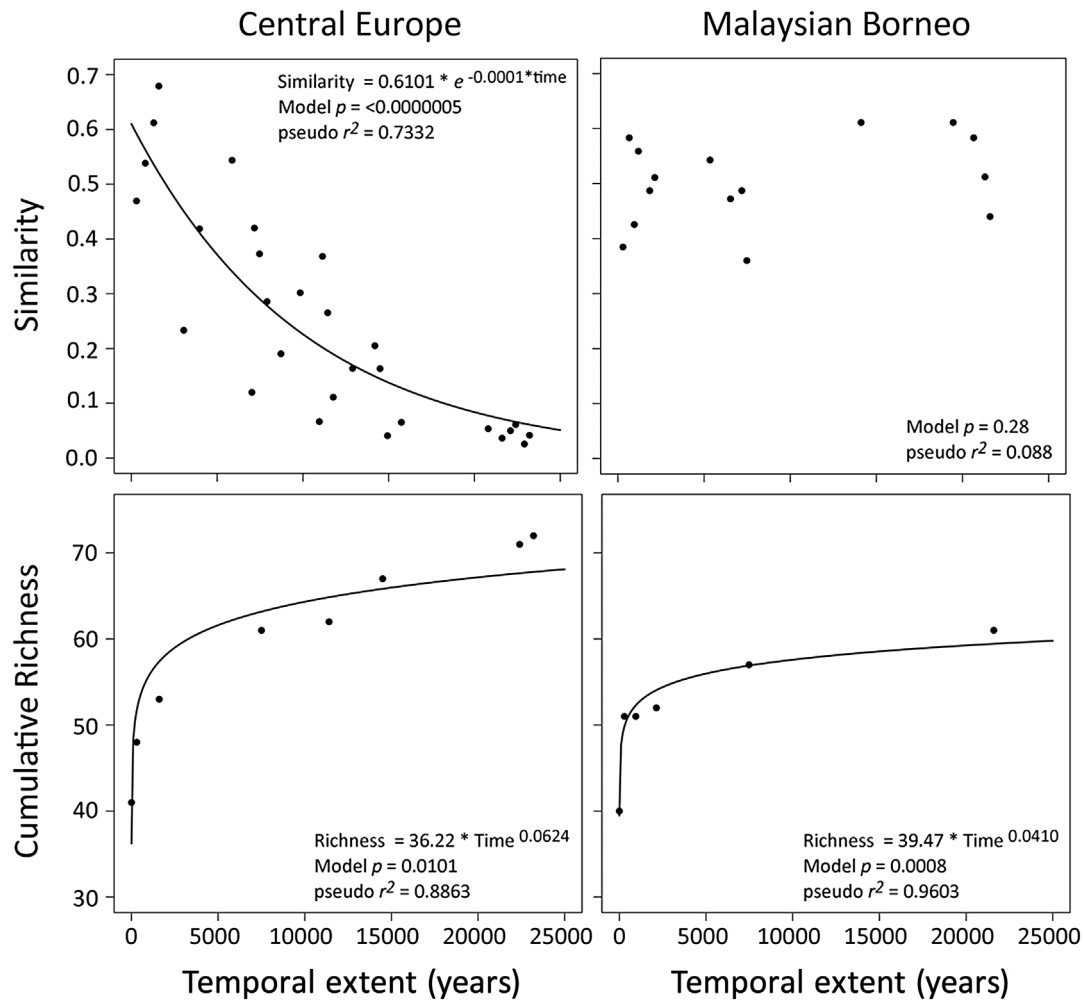


Figure 1. Comparison of temporal community composition changes for central European temperate and Malaysian wet tropic land snail communities. (Top row) Distance decay over the modern to LGM transition based on all pairwise sample comparisons. (Bottom row) Species–time relationship across 0 (modern) to 25 ka extents.

data, however, given known palynological changes from seasonally dry to wet tropical forest over the analyzed temporal extent (Jones et al. 2014). Yet, community similarity only varied between 0.4–0.6 and demonstrated no significant trend across 0.3–25 ka extents. These similarity values are equivalent to those observed between adjacent (10 km) modern karst tower faunas at Simbaluyon and Tinahas, Malaysia (48 and 45 observed species, respectively, with 36 in common) and are likely driven by stochastic differences between samples drawn from the same regional pool (Preston 1962).

It is not immediately clear why land snail community composition in the tropics has been more resilient to long-term regional climate change than that observed for vascular plants in the same region. We hypothesize that this may be related to the: 1) smaller habitat size required to sustain minimally viable land snail populations – ranging down to 10-m² areas for some microsnaills (Schilthuizen 2011), and/or 2) excellent passive dispersal abilities of many land

snaills (Gittenberger et al. 2006) which allow them access to even the most isolated refugia. Thus an archipelago of tiny refugia within the karst-tower landscape may provide long-term buffering against moderate temperature and considerable precipitation variability, helping maintain a uniform regional species pool over long time scales. The temporal turnover seen in the temperate zone, however, probably reflects the greater total experienced temperature and precipitation variation which exceeded the ability of such tiny, local refugia to buffer regional climate change.

Lastly, even though land snail communities are among the clearest examples known for neutral community assembly (Schilthuizen 2011), we note that these data provide no clear evidence for directional stochastic compositional change (aka ‘ecological drift’ of Hubbell 2001) over time. Thus even though such drift can be generated in mesocosm experiments over short time scales (Gilbert and Levine 2017) it is unclear that this process is important in natural systems.

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Supplementary material (Appendix ecog-03996 at <www.ecography.org/appendix/ecog-03996>). Appendix 1–4.

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Appendix 1

Site and community composition data

Tropical data represents samples collected at six different depths from a karst fill in wet tropical forest at Niah, Malaysia (Barker et al. 2003). The analyzed eight temperate samples were generally collected from tufa-depositing wooded springs within a 130 km extent in a faunistically-homogenous area of SW Slovakia and SE Czech Republic in central Europe. Because no single site continuously accumulated sediments over the last 25 ka, multiple sites were required to generate a temporal transect of similar extent. As LGM spring deposits are absent due to the cold and very dry climate (Ložek 1964), the two oldest samples represent characteristic loess assemblages present in the region.

Shells were removed using standard protocols and identified to species. Total abundance for each species was then determined. At Niah, 40 species were encountered in the modern sample, with a total of 61 species and 6100 individuals being observed over the 25 ka modern to LGM transect. For the Slovakia/Czech Republic data, 41 species were encountered in the modern sample with a total of 72 species and 8330 individuals being observed over the 25ka modern to LGM transect.

Niah (3°48'N, 113°48'E)

Contemporary material was sampled by collecting ten litres of soil, litter and debris along a length of 10 m at the foot of a ca 5-m-tall limestone rock face with inclination between 40° and 60°. Subfossil samples were collected via five-litre sediment samples (N1041, N1043, N1032, N1006, N1009) at Lobang Hangus, one of the eastern cave entrances of the Gunung Subis limestone massif (Szabó 2016). All shells were identified to species / morphospecies using Liew (2012) and Vermeulen et al. (2015). To avoid recording different fragments of the same individual, only specimens with an intact protoconch were counted. All samples are stored in the Naturalis Biodiversity Center, Leiden, under collection reference numbers RMNH.MOL.333904-

RMNH.MOL.334035, RMNH.MOL.335095-335108, RMNH.MOL.336255-RMNH.MOL.336292,
 RMNH.MOL.337806-RMNH.MOL.337848, and RGM.1007839-RGM.1008004.

Table 1. Niah species data

Species	Niah					
	(modern)	N1041	N1043	N1032	N1006	N1009
<i>Acmella nana</i>	3	0	0	0	0	0
<i>Acmella polita</i>	0	0	0	0	1	0
<i>Acmella striata</i>	1	5	2	0	0	1
<i>Allopeas clavulinus</i>	14	107	60	160	198	392
<i>Allopeas gracile</i>	107	1278	130	329	80	72
<i>Alycaeus jagori</i>	6	3	1	8	15	33
<i>Amphidromus</i> sp. 1	0	1	0	0	0	0
<i>Anaglyphula</i> sp. 1	0	1	0	0	0	0
<i>Arinia pseudopomatias</i>	4	0	0	0	0	0
<i>Arinia</i> sp. 1	1	0	0	0	0	0
<i>Beilania philippinensis</i>	0	0	0	0	12	24
<i>Boysidia salpinx</i>	0	22	8	9	22	62
<i>Camaenid</i> sp. 1	1	0	3	1	1	2
<i>Camaenid</i> sp. 2	1	0	0	0	0	0
<i>Chamalycaeus specus</i>	12	43	11	13	18	16
" <i>Charopa</i> " " <i>argos</i> "	0	61	11	19	76	101
" <i>Charopa</i> " " <i>jugalis</i> "	0	0	0	0	0	1
<i>Craspedotropis</i> sp. 1	0	0	0	0	2	0
<i>Cyclophorid</i> sp. 1	0	1	0	0	0	0
<i>Diplommatina concinna</i>	0	0	0	0	0	1
<i>Diplommatina maduana</i>	0	0	0	1	0	0
<i>Diplommatina niahensis</i>	69	5	5	1	2	3
<i>Diplommatina strongyla</i>	0	9	4	18	31	79
<i>Diplommatina subisensis</i>	1	0	0	0	1	2
<i>Elasmias manilense</i>	1	2	0	0	0	0
<i>Everettia</i> sp. 1	8	0	2	0	0	0
<i>Georissa niahensis</i>	5	0	0	1	3	7
<i>Georissa</i> sp. 1	1	0	2	14	0	2
<i>Geotrochus heraclea</i>	0	1	0	0	0	0
<i>Japonia</i> sp. 1	2	0	0	2	0	0
<i>Japonia</i> sp. 3	1	0	0	0	0	0
<i>Japonia</i> sp. 4	3	0	0	0	0	0
<i>Japonia</i> sp. 5	0	1	0	0	0	0
<i>Kaliella accepta</i>	1	0	3	3	0	0
<i>Kaliella doliolum</i>	2	616	25	41	24	2
<i>Kaliella microconus</i>	4	22	11	6	35	79
<i>Kaliella scandens</i>	7	5	3	1	0	35
<i>Leptopoma pellucidum</i>	0	1	1	0	0	0
<i>Macrochlamys tersa</i>	1	0	0	1	0	1
<i>Microcystina lissa</i>	1	8	0	3	13	10
<i>Microcystina microrhynchus</i>	71	20	12	33	24	11
<i>Microcystina</i> sp. BO-08	1	1	0	0	1	0
<i>Microcystina striatula</i>	4	0	0	0	0	0
<i>Opisthoporus</i> sp. 1	0	0	0	0	3	0

<i>Opisthostoma brachyacrum</i>	62	65	105	284	32	142
<i>Opisthostoma cookei</i>	7	1	0	2	2	3
<i>Opisthostoma hosei</i>	28	18	17	12	5	3
<i>Opisthostoma stellasubis</i>	2	0	0	0	0	0
<i>Paropeas achatinaceum</i>	27	0	0	0	0	0
<i>Phaedusa borneensis</i>	0	1	4	0	2	15
<i>Philalanka tambunanensis</i>	0	1	1	0	0	0
<i>Philalanka kusana</i>	6	1	9	17	26	99
<i>Philalanka moluensis</i>	0	0	0	0	0	15
<i>Pterocyclos</i> sp. 1	3	0	1	0	0	0
<i>Ptychopatala circumlitum</i>	0	0	0	0	11	0
<i>Ptychopatala orcella</i>	0	0	0	0	0	9
<i>Ptychopatala orcula</i>	1	7	0	1	0	0
<i>Pupina hosei</i>	4	0	0	0	0	0
<i>Pupisoma pulvisculum</i>	5	12	1	0	0	15
<i>Subulina octona</i>	10	0	0	0	0	0
<i>Videna</i> sp. 1	3	0	0	1	0	0

Slovakia/Czech Republic

In an attempt to parallel Niah temporal sampling, subfossil faunas were documented from five sites: the modern fauna from the Kalábová fen (48°56'N, 17°44'E), early to late Holocene from the Mituchovci fen (48°56'N, 17°58'E), late glacial from the Santovka fen (48°09'N, 18°45'E), and LGM loess faunas from Čata (47°57'N, 18°39'E) and Pod Tureckom (48°48'N, 17°51'E). All samples were collected and processed using standardized procedures (Ložek 1964), with shells being identified to species using Ložek (1964), and Horsák et al. (2013). Further collection details are provided in references provided in Supplementary Materials 2.

Table 2. Slovakia/Czech Republic species data. Note that only presence/absence data is reported from Pod Tureckom.

Species	Kal	Mit1	Mit2	Mit3	Mit4	San	Čata	Tur
<i>Acanthinula aculeata</i>	15	9	21	8	0	0	0	0
<i>Aegopinella epipedostoma</i>	0	0	0	7	0	0	0	0
<i>Aegopinella minor</i>	76	2	22	16	0	0	0	0
<i>Aegopinella pura</i>	156	24	117	54	3	0	0	0
<i>Alinda biplicata</i>	12	2	36	14	0	0	0	0
<i>Arianta arbustorum</i>	37	0	5	10	3	0	0	0
<i>Carychium minimum</i>	127	124	50	98	5	0	0	0
<i>Carychium tridentatum</i>	696	36	93	372	29	0	0	0
<i>Causa holosericea</i>	0	0	0	1	0	0	0	0
<i>Cepaea hortensis</i>	1	0	1	0	0	0	0	0
<i>Clausilia dubia</i>	0	0	0	1	10	0	0	*
<i>Clausilia pumila</i>	0	0	0	5	3	1	0	0
<i>Clausilia rugosa</i>	0	0	1	2	0	0	0	0
<i>Cochlicopa lubrica</i>	61	139	7	29	2	4	0	0
<i>Cochlicopa lubricella</i>	0	0	0	0	0	4	0	0

<i>Cochlodina laminata</i>	1	0	2	0	0	0	0	0
<i>Columella columella</i>	0	0	0	0	0	0	119	0
<i>Columella edentula</i>	25	0	4	14	0	0	0	0
<i>Daudebardia brevipes</i>	2	0	10	0	0	0	0	0
<i>Daudebardia rufa</i>	37	3	12	0	0	0	0	0
<i>Discus perspectivus</i>	0	0	84	75	0	0	0	0
<i>Discus rotundatus</i>	4	1	17	46	0	0	0	0
<i>Discus ruderatus</i>	0	0	0	1	85	0	0	0
<i>Ena montana</i>	0	0	0	2	0	0	0	0
<i>Euconulus alderi</i>	0	0	0	0	0	2	0	0
<i>Euconulus fulvus</i>	30	6	24	0	22	0	0	0
<i>Faustina faustina</i>	49	0	0	0	0	0	0	0
<i>Fruticicola fruticum</i>	0	2	5	3	0	0	0	0
<i>Helicodonta obvoluta</i>	6	1	1	1	0	0	0	0
<i>Helicopsis striata</i>	0	0	0	0	0	2	52	0
<i>Helix pomatia</i>	2	1	1	1	0	0	0	0
<i>Isognomostoma isognomostomos</i>	11	0	1	3	0	0	0	0
<i>Macrogastra plicatula</i>	0	0	16	4	0	0	0	0
<i>Macrogastra tumida</i>	32	0	32	0	0	0	0	0
<i>Macrogastra ventricosa</i>	75	3	5	0	0	0	0	0
<i>Merdigera obscura</i>	1	0	0	0	0	0	0	0
<i>Monachoides incarnatus</i>	194	1	7	3	0	0	0	0
<i>Monachoides vicinus</i>	31	0	0	0	0	0	0	0
<i>Nesovitrea hammonis</i>	3	23	7	0	9	2	0	0
<i>Nesovitrea petronella</i>	0	0	0	0	16	0	0	0
<i>Orcula dolium</i>	0	0	7	7	0	0	0	0
<i>Oxychilus cellarius</i>	0	2	7	0	0	0	0	0
<i>Oxychilus glaber</i>	2	1	4	0	0	0	0	0
<i>Oxyloma elegans</i>	2	59	2	0	0	5	0	0
<i>Perforatella bidentata</i>	26	3	19	68	10	0	0	0
<i>Petasina unidentata</i>	30	0	1	0	0	0	0	0
<i>Platyla polita</i>	0	4	15	26	3	0	0	0
<i>Plicuteria lubomirskii</i>	0	0	1	0	0	0	0	0
<i>Punctum pygmaeum</i>	90	28	4	1	16	2	0	0
<i>Pupilla alpicola</i>	0	0	0	0	0	47	271	*
<i>Pupilla loessica</i>	0	0	0	0	0	0	0	*
<i>Pupilla muscorum</i>	0	0	0	0	0	0	491	*
<i>Pupilla sterrii</i>	0	0	0	0	0	0	449	*
<i>Pupilla triplicata</i>	0	0	0	0	0	0	337	0
<i>Sphyradium doliolum</i>	0	0	0	3	0	0	0	0
<i>Succinea putris</i>	5	0	0	0	0	1	0	0
<i>Succinella oblonga</i>	1	0	14	62	1	16	397	*
<i>Trochulus hispidus</i>	1	0	0	0	0	0	158	*
<i>Trochulus villosulus</i>	0	0	0	3	0	0	0	0
<i>Vallonia costata</i>	0	15	2	162	51	7	0	0
<i>Vallonia pulchella</i>	2	144	7	0	0	18	0	0
<i>Vallonia tenuilabris</i>	0	0	0	0	0	6	165	*
<i>Vertigo angustior</i>	0	1	0	27	1	0	0	0
<i>Vertigo antivertigo</i>	0	43	1	0	0	0	0	0
<i>Vertigo pusilla</i>	2	0	4	10	0	0	0	0
<i>Vertigo pygmaea</i>	10	103	6	0	0	7	21	0
<i>Vertigo substriata</i>	87	3	14	216	11	0	0	0

<i>Vestia turgida</i>	30	0	3	200	33	0	0	0
<i>Vitrea contracta</i>	17	0	36	0	0	0	0	0
<i>Vitrea crystallina</i>	16	2	5	98	131	0	0	0
<i>Vitrea diaphana</i>	22	0	22	5	0	0	0	0
<i>Zonitoides nitidus</i>	0	5	57	7	0	0	0	0

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Appendix 2

Chronometric dating

Niah dates were based on AMS ^{14}C dating of *Kaliella* shells, given that its family (Euconulidae) is known to principally use metabolically derived carbon for shell construction (Pigati et al. 2010). ^{14}C analysis was carried out by Aeon Laboratories, Tucson, Arizona. Samples were pre-cleaned by removing all soil and other non-shell particles, and then subjected to Accelerator Mass Spectrometry. ^{14}C years were converted to calendar years with the program CALIB ver. 6, using the INTCAL13 dataset for terrestrial samples (Reimer et al. 2013). Dates used for analyses represent the median value within the observed range.

Sample	Species	No. shells	F ^{14}C ^(b)	^{14}C age (year BP)	SD (year)	Calibrated age, 2-sigma range (year BP)
Niah (modern)	<i>K. doliolum</i> + <i>K. scandens</i> + <i>K. microconus</i>	11	0.9203	665	± 20	670–563
N1041	<i>K. doliolum</i>	20	0.8832	1,000	± 70	1060–760
N1043	<i>K. doliolum</i>	21	0.8136	1,655	± 20	1606–1527
N1032	<i>K. doliolum</i>	41	0.7211	2,625	± 20	2768–2740
N1006	<i>K. doliolum</i>	24	0.4032	7,295	± 30	8173–8027
N1009	<i>K. doliolum</i> + <i>K. scandens</i>	20	0.1014	18,380	± 80	22 450–21 980

Slovakia/Czech Republic

Sample dating was based on AMC ^{14}C analysis for late-glacial to Holocene material using embedded organic material and optically-stimulated luminescence for LGM loess deposits which lacked organic material. Sample-specific information regarding dating may be found in the following references:

Map code	Site	Source	Median calibrated (years BP)
Kal	Kalábová	Dvořáková et al. 2011	modern
Mit	Mituchovci	Frodlová et al. 2017	299
	Mituchovci	Frodlová et al. 2017	1600
	Mituchovci	Frodlová et al. 2017	7470
	Mituchovci	Frodlová et al. 2017	11442
San	Santovka	Šolcová et al. (unpubl. data)	14494
Cat	Čata	Hošek et al. 2017	22400
Tur	Pod Tureckom	Vlačiky et al. 2013	23210

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Appendix 3

Statistical methods

The turnover and nestedness components of beta diversity were computed based on Baselga (2010) using binary Jaccard dissimilarity. Temporal distance decay (DD) and species–time relationship (STR) analyses were conducted on both datasets. DD plots were generated by calculating separately in each region temporal distance and Jaccard similarity between all pairwise sample combinations (Nekola and White 1999). Because DD may be modeled through either exponential or power law decay (Nekola and McGill 2014), two-parameter versions of each functional form were fit to the data using non-linear regression. The best-fit model to the data was determined using the small sample-size corrected Akaike information criterion (AICc). STR was determined from modern to the most ancient sample, with a power law accumulation curve being fit to the data using non-linear regression. For both analyses, model significance and pseudo- r^2 were calculated for each region, with best fit parameters being reported for significant models.

All statistical analyses were conducted in R ver. 3.4.1 (<www.r-project.org>). For both DD and STR best fit non-linear models were fit using the NLS package, which uses a relative-offset convergence criterion that compares the numerical imprecision at the current parameter estimates to the residual sum-of-squares.

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Appendix 4

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