

Biogeographic clustering of gastropod presence-absence data with spatial genetics freeware, exemplified for Northrhine-Westphalia, Germany

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Abstract: The study explores if the spatial structure of presence-absence data from faunal surveys can be analyzed with genetics freeware. This is exemplified for distribution data of terrestrial gastropods from Northrhine-Westphalia, Germany, using the packages Structure and Geneland. The output differs between the approaches used by the programs. Structure, that assigns data points to probabilities to pertain to a given population was not explicitly developed for spatial analyses, seems to group mainly by species richness and resulted in a mosaic-like pattern of the group assignments. Geneland, that was explicitly developed for spatial analyses, revealed two spatially well separated groups. The turnover between the two groups roughly occurred at an altitude of 100-150 m a. s. l. and traditional biogeographic (sub-)regions.

Keywords: binary data, biogeography, diversity, forest, Gastropoda, Geneland, nestedness, structure

Zusammenfassung: Die Studie testet, ob die räumliche Struktur von Präsenz-Absenz-Daten aus faunistischen Erfassungen mit Freeware für genetische Populationsstrukturen analysiert werden kann. Dies wird beispielhaft an den Verbreitungsdaten terrestrischer Gastropoden aus Nordrhein-Westfalen und den Programmen Structure und Geneland gezeigt. Die Ergebnisse differieren, da die Programme unterschiedliche Ansätze benutzen. Structure weist Datenpunkten eine Wahrscheinlichkeit zu, zu einer Population zu gehören und wurde nicht für räumliche Analysen entwickelt. Das Programm schien hauptsächlich nach Artenreichtum zu separieren und das Ergebnis resultierte in einer eher mosaikartigen räumlichen Anordnung der Gruppenzugehörigkeiten. Geneland, das extra für räumliche Analysen konzipiert wurde, separierte hingegen zwei großflächigere Gruppen. Die Grenze zwischen den beiden Gruppen verlief in etwa auf der Höhe von 100-150 m NN und traditionellen biogeographischen (Sub-)Regionen.

Introduction

The classical biogeographic regions are based on manual classification of areas of taxonomical similarity and delimitation of these areas on maps. Here, regional species turnover is explored using computer programs without a-priori assumptions on the location of the turnover. The lack of a-priori assumptions is one characteristic of plotting spatial genetic data. Because genetic diversity metrics basically can be treated in a similar way to species diversity metrics (e. g. GREGORIUS 2010, GAGGIOTTI & al. 2018), the performance of two freeware programs that originally were developed for spatial genetic analyses are compared. The following questions are addressed:

- (1) Can programs for spatial genetic analyses also be used for the analysis of the presence-absence data of faunal surveys?
- (2) If the two programs differ in the output, i. e., in the interpretation of the data, then why?
- (3) Can a main turnover be detected, and does it coincide with classical biogeographic borders?

Material and Methods

Field data

Data originated from the mapping survey of the Mollusca of the German federal state Northrhine-Westphalia (NRW, Fig. 1), Germany, census 1.1.2008. The spatial structure of the mollusc data is based on the individual maps from the topographical map series scaled 1:25,000 with each individual map split into four quadrants. Each quadrant covers ca. 31.25 km² and was treated as a raster point. The numbers of the map series plus the quadrant number are used as coordinate system. To give an example, 5110 Q* translates to x = 10, with 0.5 added if Q* is one of the eastern quadrants 2 and 4, and y = 51, with 0.5

added if Q^* is one of the southern quadrants 3 and 4. Or, to be more specific, 4612 Q2 translates to $x = 12.5$, $y = 46$, or 4208 Q4 is $x = 08.5$, $y = 42.5$.

The focus was on the terrestrial gastropods, thus aquatic molluscs were deleted from the data set. Species that occurred in less than twenty raster points of a total of 1128 possible raster points were also omitted, as their absence is non-informative, whereas their presence may be accidental or a sampling effect. Many of them are known to be local introductions. Also, widespread species (more than 403 raster points, corresponding to non-informative conserved genes) and *Deroceras invadens* REISE & al. 2011, an anthropogenically spread species with rapid eastward range expansion in NRW between 2000 and 2010, were omitted from the analysis because presence or absence is non-informative as well. If there is any large-scale geographical information in the data set, it should be in the set of species that occur at intermediate constancy. Raster points with zero species after all omissions were retained. As a result, the analyses are based on 1128 rasters and 61 species (= 68808 data points).



Fig. 1: Topography of Northrhine-Westphalia (file 20081002172026!North_Rhine-Westphalia_Topography_05 from Wikipedia; author: TUBS 2008, CC Attribution-Share Alike 4.0 International).

Analysis

The analyses were run in Structure 2.2 (PRITCHARD & al. 2000, FALUSH & al. 2005) and in Geneland 2.0.12 (GUILLOT & al. 2005a, b). Both freeware programs are suitable for binary data because they would consider continuous, different values such as abundance data as a completely different (allelic) state of the species, and not as an ecological gradient of carrying capacity for the species. Species thus were entered as presence-absence data, which thus corresponds to genes with two alleles per locus.

Yet, the two programs differ in their approach. Structure calculates distance matrices. The output is a group assignment probability based on similar faunal composition (“populations” in terms of the genetic programs).

In contrast, Geneland was explicitly designed to infer the number of populations and the spatial location of genetic discontinuities between those populations from data sets containing geo-referenced individual multilocus genotypes (GUILLOT & al. 2005a, b). The result is a map that shows the distribution ranges of groups of similar faunal composition (in genetic terms: the populations). Transferred to the context of species assemblages, this allows the detection of areas with high species turnover, i. e. the borders between habitats or biomes as perceived by the assemblages. The raster points were thus considered as “individuals”, having a set of species (“alleles”) characterizing its “genotype”, and the spatial context is included in calculating the groups (“populations”).

The analyses of the field data were run with the data set being treated as haploid. The number of populations was set to two to focus on the main gradient. Also, the occurrence of some species is correlated (corresponding to “linkage disequilibrium”) for which the number of populations should be predefined to prevent the inference of spurious populations (GUILLOT & al. 2005b). All other parameters were left at default settings. The analysis in Structure was set to a Burn-in period of 1000, with 100,000 MCMC repetitions. The large number of species significantly slowed down the calculation process in Geneland. Hence, the analysis was restricted to 1000 iterations, any 10th of which was saved. The outputs of both programs were plotted in a x,y-graph.

Species richness per group-specific area (raster points) was compared using rarefaction analysis with 50 permutational runs in EstimateS 7.5.1 (COLWELL 2005), the comparison of means was done in Statistica 6.1 (StatSoft Inc, Tulsa, USA).

Results

Structure

Structure assigned 784 raster points to group 1 (with a probability > 50 %), and 344 raster points to group 2 (> 50 %). The resulting graph indicates a NNW-SSE gradient in the assignment. Additionally, a few geographical structures were resolved, such as the long stretch of the Teutoburg Ridge in the NE (Fig. 2). The assignment seems to be based on a nested species set.

Group 1 lacked characteristic species (Tab. 1), whereas group 2 was related to a mixed set of forest-associated and calciphilous species. Group 2 comprised acidification-tolerant forest species such as *Lehmannia marginata* and *Malacolimax tenellus*, species that typically show affinities towards calcareous beech forests and wooded carbonate outcrops such as *Helicodonta obvoluta* and *Helicigona lapicida*, and species with affinities to calcareous open habitats such as *Vallonia pulchella*, *Pupilla muscorum*, *Cecilioides acicula* and *Helicella itala*. A between-group-difference was also found for widespread species that were not included in the original analysis (Tab. 1).

The probability of a raster point to be assigned to group 2 increased with its species richness. As a result, the area assigned to group 2 (probability > 0.5) harbored more taxa than the same area of group 1 (rarefaction analysis of the raster data: 132 ± 5 species vs. 113 ± 4 species at 344 raster points, $P < 0.0001$).

Geneland

The mosaic-like pattern was smoothed in Geneland. This program assigned 645 raster points to group 1 and 483 raster points to group 2. Unlike Structure, for which the result remained mosaic-like when shifting the probability threshold to 0.8, Geneland clearly depicted a transition that roughly mirrors that between the mountains of the Teutoburg Ridges, the Weserbergland, and the northern part of the Rhenish Shield on the one hand (= group 2) and the plains on the other hand (group 1; Fig. 2).

The lower altitudes are severely transformed by human impact and are predominantly inhabited by widespread species, resulting in an increased number of raster points with the absence of the species used in the analysis. Additionally, the lower altitudes are characterized by species that are typical for the remains of floodplains and wetlands (Tab. 1). In contrast, group 2 comprises a set of species with mountainous affinities (e. g., *Eucobresia diaphana*, *Phenacolimax major*) together with forest-associated species such as *Limax cinereoniger*, including those of floodplain forests (e. g., *Arion silvaticus*, *Cochlodina laminata*), and hard substrate grazing specialists (such as *Clausilia rugosa parvula*, *Helicigona lapicida*; Tab. 1).

Tab. 1: Species that were typical for group 1 or 2 in the two analyses (mean and standard deviation of the occurrences). Species for group 2 were restricted to those with a t-value ≤ -10 in the comparison of means test. *: species were originally omitted from the analysis, as they were either too rare or too frequent. Degrees of freedom (df) = 1126. Systematics follow WIESE (2016).

Species	Structure				Geneland			
	Group 1	Group 2	t	p	Group 1	Group 2	t	p
typical for group 1 (only where at least once marginally significant)								
<i>Oxyloma sarsii</i> (ESMARK & HOYER 1886)	0.03±0.16	0.03±0.18	-0.6	0.541	0.04±0.20	0.01±0.09	3.4	< 0.001
* <i>Zonitoides nitidus</i> (O. F. MÜLLER 1774)	0.49±0.50	0.55±0.50	-2.0	0.044	0.54±0.50	0.47±0.50	2.4	0.016
* <i>Vertigo moulinsiana</i> (DUPUY 1849)	0.01±0.12	0.02±0.13	-0.4	0.665	0.02±0.15	0.01±0.08	2.1	0.035
* <i>Zonitoides excavatus</i> (ALDER 1830)	0.01±0.08	0.00±0.00	1.5	0.138	0.01±0.09	0.00±0.00	1.9	0.052
typical for group 2 (only where $t \leq -10$)								
* <i>Arion rufus</i> (LINNAEUS 1758)	0.33±0.47	0.91±0.29	-21.2	< 0.001	0.29±0.45	0.80±0.40	-19.5	< 0.001
<i>Cochlodina laminata</i> (MONTAGU 1803)	0.11±0.31	0.58±0.49	-19.6	< 0.001	0.10±0.30	0.46±0.50	-15.0	< 0.001
<i>Phenacolimax major</i> (FÉRUSAC 1807)	0.07±0.26	0.52±0.50	-19.5	< 0.001	0.05±0.22	0.42±0.49	-16.9	< 0.001
<i>Clausilia rugosa parvula</i> (FÉRUSAC 1807)	0.02±0.13	0.35±0.48	-18.3	< 0.001	0.00±0.04	0.28±0.45	-15.6	< 0.001
<i>Limax cinereoniger</i> WOLF 1803	0.10±0.30	0.54±0.50	-18.1	< 0.001	0.03±0.18	0.51±0.50	-22.4	< 0.001
<i>Lehmanna marginata</i> (O. F. MÜLLER 1774)	0.12±0.32	0.56±0.50	-17.7	< 0.001	0.11±0.31	0.45±0.50	-14.2	< 0.001
* <i>Aegopinella pura</i> (ALDER 1830)	0.32±0.47	0.82±0.38	-17.6	< 0.001	0.27±0.45	0.73±0.44	-17.0	< 0.001
<i>Malacolimax tenellus</i> (O. F. MÜLLER 1774)	0.11±0.32	0.54±0.50	-17.3	< 0.001	0.09±0.29	0.44±0.50	-14.9	< 0.001
<i>Helicigona lapicida</i> (LINNAEUS 1758)	0.04±0.20	0.39±0.49	-16.9	< 0.001	0.02±0.13	0.32±0.47	-15.8	< 0.001
<i>Vallonia pulchella</i> (O. F. MÜLLER 1774)	0.20±0.40	0.65±0.48	-16.3	< 0.001	0.24±0.43	0.48±0.50	-8.7	< 0.001
<i>Acanthinula aculeata</i> (O. F. MÜLLER 1774)	0.10±0.30	0.48±0.50	-16.1	< 0.001	0.14±0.34	0.32±0.47	-7.6	< 0.001
<i>Helicodonta obvoluta</i> (O. F. MÜLLER 1774)	0.02±0.15	0.32±0.47	-16.0	< 0.001	0.01±0.10	0.25±0.43	-13.6	< 0.001
<i>Arion silvaticus</i> LOHMANDER 1937	0.22±0.41	0.66±0.47	-15.9	< 0.001	0.18±0.39	0.58±0.49	-15.2	< 0.001
* <i>Oxychilus cellarius</i> (O. F. MÜLLER 1774)	0.36±0.48	0.81±0.39	-15.6	< 0.001	0.35±0.48	0.70±0.46	-12.5	< 0.001
<i>Cecilioides acicula</i> (O. F. MÜLLER 1774)	0.05±0.21	0.36±0.48	-15.1	< 0.001	0.08±0.27	0.23±0.42	-6.9	< 0.001
* <i>Cepaea hortensis</i> (O. F. MÜLLER 1774)	0.42±0.49	0.86±0.34	-15.0	< 0.001	0.40±0.49	0.77±0.42	-13.6	< 0.001
<i>Pupilla muscorum</i> (LINNAEUS 1758)	0.03±0.18	0.33±0.47	-15.0	< 0.001	0.06±0.23	0.21±0.41	-8.2	< 0.001
* <i>Punctum pygmaeum</i> (DRAPARNAUD 1801)	0.33±0.47	0.76±0.42	-14.9	< 0.001	0.33±0.47	0.63±0.48	-10.4	< 0.001
* <i>Monachoides incarnatus</i> (O. F. MÜLLER 1774)	0.54±0.50	0.95±0.22	-14.5	< 0.001	0.50±0.50	0.88±0.33	-14.3	< 0.001
* <i>Boettgerilla pallens</i> SIMROTH 1912	0.31±0.46	0.72±0.45	-14.1	< 0.001	0.29±0.45	0.63±0.48	-12.1	< 0.001
* <i>Euconulus fulvus</i> (O. F. MÜLLER 1774)	0.29±0.45	0.69±0.46	-13.6	< 0.001	0.26±0.44	0.61±0.49	-12.8	< 0.001
* <i>Clausilia bidentata</i> (STRØM 1765)	0.36±0.48	0.76±0.42	-13.5	< 0.001	0.36±0.48	0.64±0.48	-9.8	< 0.001
<i>Helicella itala</i> (LINNAEUS 1758)	0.05±0.21	0.31±0.46	-13.2	< 0.001	0.04±0.20	0.24±0.43	-10.5	< 0.001
* <i>Helix pomatia</i> LINNAEUS 1758	0.31±0.46	0.70±0.46	-13.2	< 0.001	0.30±0.46	0.60±0.49	-10.4	< 0.001
<i>Eucobresia diaphana</i> (DRAPARNAUD 1805)	0.06±0.24	0.34±0.48	-13.1	< 0.001	0.01±0.12	0.33±0.47	-16.3	< 0.001
* <i>Aegopinella nitidula</i> (DRAPARNAUD 1805)	0.63±0.48	0.97±0.17	-12.7	< 0.001	0.62±0.49	0.89±0.32	-10.6	< 0.001
* <i>Merdigera obscura</i> (O. F. MÜLLER 1774)	0.22±0.41	0.57±0.50	-12.6	< 0.001	0.24±0.43	0.43±0.50	-6.9	< 0.001
* <i>Deroceras reticulatum</i> (O. F. MÜLLER 1774)	0.42±0.49	0.80±0.40	-12.3	< 0.001	0.41±0.49	0.71±0.46	-10.4	< 0.001
<i>Ena montana</i> (DRAPARNAUD 1801)	0.03±0.18	0.26±0.44	-12.3	< 0.001	0.01±0.11	0.23±0.42	-12.4	< 0.001
<i>Arion circumscriptus</i> JOHNSTON 1828	0.17±0.38	0.51±0.50	-12.2	< 0.001	0.15±0.36	0.44±0.50	-11.3	< 0.001
* <i>Discus rotundatus</i> (O. F. MÜLLER 1774)	0.69±0.46	0.99±0.09	-12.0	< 0.001	0.66±0.47	0.94±0.23	-12.2	< 0.001
<i>Daudebardia rufa</i> (DRAPARNAUD 1805)	0.01±0.11	0.19±0.39	-11.7	< 0.001	0.00±0.06	0.15±0.36	-10.2	< 0.001
* <i>Vitrina pellucida</i> (O. F. MÜLLER 1774)	0.52±0.50	0.86±0.34	-11.5	< 0.001	0.51±0.50	0.78±0.41	-9.9	< 0.001
<i>Limax maximus</i> LINNAEUS 1758	0.19±0.39	0.50±0.50	-11.4	< 0.001	0.24±0.42	0.34±0.48	-4.0	< 0.001
* <i>Arion distinctus</i> J. MABILLE 1868	0.38±0.49	0.72±0.45	-11.1	< 0.001	0.35±0.48	0.66±0.47	-10.7	< 0.001
* <i>Nesovitrea hammonis</i> (STRØM 1765)	0.50±0.50	0.83±0.37	-11.0	< 0.001	0.49±0.50	0.75±0.43	-9.1	< 0.001
* <i>Cochlicopa lubrica</i> (O. F. MÜLLER 1774)	0.66±0.47	0.94±0.23	-10.5	< 0.001	0.67±0.47	0.85±0.36	-7.2	< 0.001
<i>Macrogastra plicatula</i> (DRAPARNAUD 1801)	0.02±0.13	0.18±0.38	-10.5	< 0.001	0.00±0.07	0.15±0.36	-10.1	< 0.001
* <i>Vitrea crystallina</i> (O. F. MÜLLER 1774)	0.39±0.49	0.72±0.45	-10.5	< 0.001	0.40±0.49	0.62±0.49	-7.5	< 0.001
<i>Vertigo pygmaea</i> (DRAPARNAUD 1801)	0.21±0.41	0.50±0.50	-10.4	< 0.001	0.25±0.44	0.36±0.48	-3.8	< 0.001
<i>Tandonia rustica</i> (MILLET 1843)	0.01±0.10	0.15±0.36	-10.3	< 0.001	0.00±0.07	0.12±0.33	-8.8	< 0.001
* <i>Carychium tridentatum</i> (RISSO 1826)	0.49±0.50	0.80±0.40	-10.0	< 0.001	0.47±0.50	0.73±0.44	-9.3	< 0.001

Geneland reproduced the main pattern in repeated runs. Yet, the assignment of many raster points southwest of the Cologne Bight (approximately $x = 05$, $y = 51$ in Fig. 1) and in the northeastern Weserbergland Mountains (approximately $x = 18$, $y = 38$ in Fig. 1) in repetitive runs was ambiguous. The former often was more or less completely included (10 out of 15 runs) and the NE part of the latter was usually excluded (13 out of 15 runs). The small area of the Beckumer Berge (approximately $x = 13$, $y = 42$ in Fig. 1) was assigned to group 2 in only two of 15 runs.

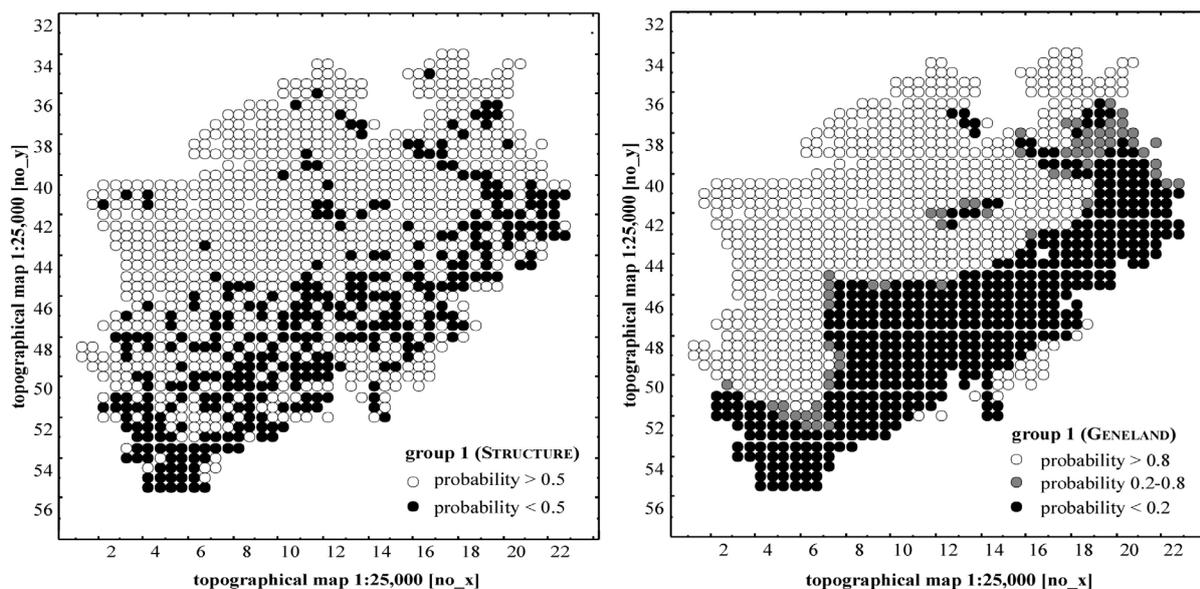


Fig. 2: Probability of the raster points to belong to one of two groups, as depicted by Structure and Geneland. Dots roughly outline the shape of the German federal state Northrhine-Westphalia (compare Fig. 1). Grid numbers refer to the numbers of the individual maps of the topographic map series 1:25,000. Only one run is exemplified for Geneland; the Lower Rhine embayment west of Cologne ($x = \text{ca. } 5, y = \text{ca. } 49$) was sometimes assigned to group 2, and the northern part of the Weserbergland ($x = \text{ca. } 19, y = \text{ca. } 38$) was sometimes assigned to group 1.

Again, there was a positive relationship between the probability of a raster point to belong to group 2 and its species richness, but the relationship was less well defined than that in Structure (data not shown). As before, the area assigned to group 2 (probability > 0.5) harbored more species than the same area of group 1 (rarefaction analysis: 131 ± 4 species vs. 118 ± 4 species at 483 raster points, $P < 0.0001$).

Discussion

The two examples support the assumption that faunal and genetic diversity metrics are interrelated and can be treated similarly (GREGORIOUS 2010, GAGGIOTTI & al. 2018). The assignment of presence-absence-data to “populations” depends on the algorithm applied. Gastropod assemblages display a nested structure across different spatial scales (e. g. BLOCH & al. 2007, and references therein). Nestedness usually occurs along gradients of habitat quality, with low-quality habitats being inhabited by only a small subset of those species occurring in high quality habitats (e. g. HYLANDER & al. 2005, HORSÁK & CERNOHORSKY 2008). When an environmental gradient is sampled, both local and regional nestedness are to be expected to occur in the data set. Structure was not explicitly developed for spatial analyses. It seemed sensitive to the species richness effects of nestedness. Geneland was explicitly developed for spatial analyses (GUILLOT & al. 2005b) and revealed larger spatially separated groups, that is, nestedness at the landscape scale.

This separation partially resembles that between the European “Atlantic” and “Continental” biogeographic regions in NRW (e. g. HINTERLANG 2018) and the traditional regional main biogeographic landscapes (“Großlandschaften”, e. g., LOHR & CONZE 2016, HINTERLANG 2018). The natural vegetation of most of the area assigned to group 1 from Geneland would be the *Deschampsia flexuosae*-Fagetum and different oak-dominated forests (TRAUTMANN & al. 1973, VERBÜCHELN & al. 1995), whereas that of group 2 would be different types of beech forests except for the lowland type with wavy hairgrass (*Deschampsia flexuosa* L.). However, the outlines of these predefined biogeographic regions were not exactly met in this study. As ANT (1963) already noted, the interpretation of the distribution of gastropods is not always simple when compared to large-scale environmental factors.

The geographic separation in Fig. 1 roughly coincides with an altitude of 100-150 m a. s. l. This altitude is depicted in Tab. 8 of ANT (1963: 61-62) as contributing most to species turnover. The most parsimonious explanations for an assemblage turnover at a given altitude are climatic factors, and temperatures

in particular (ASHCROFT & al. 2008). Indeed, temperatures show some changes in roughly the same location as the assemblage turnover (MURL 1989), whereas precipitation displays a different pattern than that of the two groups, with annual values $\leq 600 \text{ mm a}^{-1}$ (south)west of the Cologne Bight (in Fig. 1 ca. $x = 05$, $y = 52$) and $> 1000 \text{ mm a}^{-1}$ in the central and eastern parts of the mountains (ca. $x = 10$, $y = 48$, and ca. $x = 16$, $y = 47$) (e. g., HINTERLANG 2018).



Fig. 3: *Limax cinereoniger* was typical for group 2, whereas it only occurs in the few remaining large old-growth forests in the lowlands and hence was very rare in group 1 (photo: H. KAPPES, April 2008, Hambacher Forst north of the former highway A4).

Group 1 and group 2 were usually assigned to raster points with a yearly mean of average daily air temperatures above, and below, $8.5\text{-}9^\circ \text{ C}$, respectively (MURL 1989). However, the area assigned to group 2 also locally spans over the warm lower terrasses of the Rhine River in the Cologne Bight, that was expected to be assigned to group 1. On the one hand, fine-scale patterns may generally not be recognized because of the trade-off between local and global smoothing (e. g., MUGGLIN & al. 1999, DUNCAN & MENGERSEN 2020). Either the algorithm or species that also occur in fragmented floodplain forests, or drifted downstream during floods, did not allow to resolve this small, intensively modified high-temperature stretch. On the other hand, fig. 2 in ANT (1963: 42) suggests higher continentality scores for the climate along this stretch of the Rhine floodplain. Its inclusion, anyhow, has surely increased the number of species of group 2 in the rarefaction analysis.

In contrast, areas with low sampling intensity may be wrongly assigned to group 1, as probably occurred in the southeastern part of the map (Fig. 1). This is a remote mountainous area close to the Hessian border where many raster points still had less than thirty known mollusc species (terrestrial and aquatic combined), which was set as minimum target for the quadrant-based data gathering. The retrieval of thirty species usually requires sampling in different habitats, and takes between two and eight hours of field work per person, depending on habitat type and environmental conditions.

As a highlight, the analysis identified a putative biogeographical island, namely the area of the Beckumer Berge in the southern central Munsterland, as is suggested by its assignment to group 2 (Fig. 1, 2). The Beckumer Berge are also a geological island of calcareous parent material from the Cretaceous period. The area is subjected to intensive, but usually not too monotonous land use and has some areas of high conservation value such as the forests Vellerner Brook and Hoher Hagen (Natura 2000-Nr. DE-4114-302). Gastropod assemblages can persist in suitable fragments for quite some time (CAMERON & POKRYSZKO 2004). Nonetheless, there is only a delay of extinction that may last for more than 100 years for small sedentary species (PALTTO & al. 2006), but only several decades in larger gastropods such as *Limax cinereoniger* (see KAPPES & al. 2009). The stenecious forest slug *L. cinereoniger* (Fig. 3) had the highest between-group difference in occurrence probability (Tab. 1) because it is restricted to large ancient forests in the lowlands (KAPPES & al. 2009). Yet, the extinction delay concept predicts that even common species will be affected in the remaining larger fragments in the long run (TILMAN & al. 1994, 1997). It may be assumed that this is not only the case for gastropods. The whole soil fauna of the Beckumer Berge island should benefit from implementing conservation concepts that include historic land uses, linear structures and the agricultural areas.

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Literature

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