Does vicariance shape biotas?
Biogeographical tests of the vicariance model in the north-west European land snail fauna

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INTRODUCTION

Since the 1970s vicariance biogeography became a major subdiscipline of biogeography (Croizat et al., 1974; Rosen, 1976, 1978; Platnick & Nelson, 1978; Nelson & Platnick, 1981; Wiley, 1981, 1988; Humphries & Parenti, 1999). Vicariance biogeography and the derivation of area relationships from taxon cladograms depends on the assumption that vicariance is the predominant diversification mode. However, an increasing number of studies have challenged the importance of vicariance (Endler, 1982a,b; Noonan, 1988; Hausdorf, 1996, 2000; Zink et al., 2000).

Usually vicariance cannot be observed directly, because this process generally takes geologic time periods. Therefore, it is important to derive predictions about observable patterns from the vicariance model. According to the vicariance model (Croizat et al., 1974; Rosen, 1976, 1978; Platnick & Nelson, 1978; Nelson & Platnick, 1981; Wiley, 1988; Humphries & Parenti, 1999), an ancestral biota was fragmented by the appearance of a barrier. The barrier interrupted the gene flow

ABSTRACT

Aim To investigate the importance of vicariance in shaping the north-west European land snail fauna.

Location North-west Europe.

Methods We tested whether there is a non-random congruence, i.e. a clustering of species ranges, using a Monte Carlo procedure with a null model that generates range data sets such that their range size distribution, the species richness distribution of the geographic cells and the spatial autocorrelation of the occurrences of a taxon approach the parameters in the real data set. Biotic elements, groups of species with similar ranges, were delimited with Model based Gaussian clustering. The prediction that closely related species belong to different biotic elements, has been tested with a chi-square test.

Results The distribution areas of the north-west European land snail species are significantly clustered as predicted by the vicariance model. One widespread and seven regional biotic elements were identified. Contrary to the predictions of the vicariance model, closely related north-west European land snail species belong significantly more often to the same biotic element than should be expected by chance.

Main conclusions The clustering of closely related north-west European land snail species within the same biotic element indicates that speciation modes other than vicariance were frequent or that the imprint of vicariance on the ranges was obscured by extensive post-speciational dispersal. Extensive dispersal may have been caused by Pleistocene climatic fluctuations. The core areas of the regionally restricted biotic elements might indicate the positions of glacial refugia of land snails.

Keywords Biogeography, biotic elements, glacial refugia, land snails, north-west Europe, speciation, vicariance.

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between the populations separated by the barrier and, consequently, this vicariance event resulted in allopatric speciation of many of the species formerly constituting the ancestral biota. In this way, two new biotas originated, separated by the barrier. By repetitions of the described process, areas of endemism with distinct biotas, i.e. with many species restricted to the individual areas, emerged. On average, the ranges of the species, which originated in the same area of endemism will be more similar to each other than to ranges of species, which originated in other areas of endemism. Thus, the vicariance model predicts a non-random congruence of species ranges (Morrone, 1994; Hausdorf, 2002). We have developed a test of this prediction (Hausdorf & Hennig, 2003b; Hennig & Hausdorf, in press). The species originating in an area of endemism form a biotic element, a group of species whose ranges are more similar to each other than to those of other such groups (Hausdorf, 2002). If speciation is the result of vicariance events, closely related species originate in different areas of endemism and, hence, belong to different biotic elements.

In the following, we investigate whether the vicariance model can account for distribution patterns in the northwest European land snail fauna by testing these two predictions. Land snails are excellent model organisms for biogeographic studies because of their low vagility. The importance of vicariance in the evolution of land snails has been discussed repeatedly (e.g. Gittenberger, 1984, 1999; Giusti & Manganelli, 1984; Hausdorf, 1996, 2000), but it has been hardly tested whether closely related species actually originated by vicariance events.

MATERIAL AND METHODS

Distribution data

Distribution maps of most land snail species present in northwest Europe from Kerney et al. (1983) were digitized using 100 km UTM grid squares. Grid cells of which more than two-thirds are covered by sea were not considered. Cells in the transition zones of the UTM grid can become very small. To get cells, which are roughly equally sized, such small cells were either fused to give cells with c. 10,000 km², or, if they are distinctly smaller than 5000 km², they were fused with neighbouring cells. The data set includes 366 species and 306 grid squares.

Distribution maps compiled by Klemm (1974) and Reischütz (1986) for Austria were used for a detailed analysis of the eastern Alpine element. The unit areas for this analysis were 20 km UTM grid squares.

Biogeographical tests of the vicariance model

We tested whether there is a non-random congruence, i.e. a clustering of species ranges with the Monte Carlo procedure proposed by Hausdorf & Hennig (2003b); Hennig & Hausdorf (in press). As test statistics the ratio between the 25% smallest and the 25% largest Kulczynski distances \(d_K = 1 - [a/(a+b) + a/(a+c)]/2\), where \(a\) denotes the number of grid squares occupied by both species, \(b\) denotes the number of grid squares occupied only by the first species and \(c\) denotes the number of grid squares occupied only by the second species] between the ranges of the examined taxa is used. The null model simulates the case in which all inhomogeneities (clustering) of the data can be attributed to the range size distribution, to varying numbers of taxa per geographic unit and to the spatial autocorrelation of the occurrences of a taxon.

If there is a significant clustering of distribution areas, biotic elements are determined using Model based Gaussian clustering as implemented in the software MCLUST (Fraley & Raftery, 1998; see also Hausdorf & Hennig, 2003b), because this method provides decisions about the number of meaningful clusters and the number of points, which cannot be assigned adequately to any cluster. Since MCLUST does not operate on a distance matrix, it is applied on the outcome of a non-metrical multidimensional scaling (Kruskal, 1964). Furthermore, MCLUST requires an initial estimation of noise, i.e. points that do not fit in any cluster, which is done by the software NNCLEAN (Byers & Raftery, 1998).

Then, the distribution of closely related species across biotic elements is investigated in a second test. Subgenera or genera, which are not divided into subgenera were considered groups of closely related species. The systematics used follows mainly the CLECOM-Project (Bank et al., 2001). The species are classified according to systematic groups (rows), and biotic elements (columns) in a cross-table. If the vicariance model holds, it should be expected that species groups are distributed uniformly across biotic elements. This corresponds to the cross-table expected under the null hypothesis of independence of rows and columns. We used the chi-square test for independence of rows and columns of the cross-table to test the vicariance model.

The tests as well as the method for the delimitation of biotic elements are implemented in the program package PRABCLUS, which is an add-on package for the statistical software R. These programs are available at http://cran.r-project.org.

RESULTS

Tests for clustering of distribution areas

The test statistics \(T\), the ratio of the sum of the 25% smallest Kulczynski distances \(d_K\) to the sum of the 25% largest Kulczynski distances between the ranges, for the north-west European land snail species data set is 0.372. \(T\) varied between 0.358 and 0.448 for 1000 artificial data sets generated under the null model (mean 0.412). Thus, \(T\) is significantly smaller \((P = 0.004)\) for the north-west European land snail species data set than should be expected under the null model. This is due to the significantly smaller sum of the smallest distances. The 25% largest distances are distances between species, which do not occur sympatrically at all \((d_K = 1.0)\) in almost all data sets.
The test indicates that the distribution areas of the north-west European land snail species are significantly clustered.

**Determination of biotic elements**

We found eight biotic elements and a noise component with PRABCLUS. The partition of the 366 north-west European land snail species is shown in a non-metric multidimensional scaling (Fig. 1; four dimensions used, stress 26.0%; the solution does not differ from the metrical multidimensional scaling). It can easily be seen that many species do not form well separated clusters. Thus, the introduction of the noise component, which includes 21% of the species, is valuable.

One of the eight clusters includes the widespread species occurring almost throughout the study area (33 species). This cluster may not be homogeneous, but might include different elements (Holarctic, Palaearctic, European, etc.) which cannot be distinguished in the present analysis because of the limitation of the study area. The other seven clusters include species with more restricted distributions. Five of these clusters have separate core areas where more than 70% of the species belonging to the biotic element occur. The geographic centres of these biotic elements are in the Pyrenees (16 species), in western Europe (37 species), in the southern Alps (Ticino) (12 species), in the eastern Alps (35 species), and in the Carpathian Mountains (30 species) (Fig. 2a). The two remaining clusters differ from these restricted biotic elements in the lack of a core area where more than 70% of the species belonging to the biotic element occur. One of the clusters is centred in the western Alps (58 species; Fig. 2b), the other in the eastern Alps-Carpathian Mountains area (68 species; Fig. 2c).

Some species which have a wide distribution range outside the study area, but occur only marginally in the study area have been wrongly classified in a geographically restricted biotic element [e.g. the Mediterranean *Cernuella virgata* (da Costa) in the western European element or the dinaric *Cochlostoma gracile* (L. Pfeiffer), *C. nanum* (Westerlund), *C. nanum* (A. J. Wagner) in the eastern Alpine element].

We varied the parameters used for the Model based Gaussian clustering (number of considered NMDS dimensions and NNCLEAN’s tuning constant K) to investigate the stability of the cluster solution. The results are largely similar for most examined values of the parameters. Under some conditions small clusters were fused with others (e.g. the Pyrenean cluster with the W-European cluster) or were included into the noise category (e.g. the S-Alpine cluster) and the two regional clusters were also sometimes included into the noise category.

**Distribution of species groups across biotic elements**

For the analysis of the distribution of closely related species across biotic elements we omitted the noise category and the cluster of the widespread species, because this cluster may not be homogeneous and because it cannot be the result of vicariance events within the study area. Furthermore, we

![Figure 1](image-url)

**Figure 1** Non-metrical multidimensional scaling (four dimensions used, only first two dimensions shown; stress 26.0%) of the range data of the north-west European land snail species. Biotic elements found with PRABCLUS: ▲ eastern Alpine-Carpathian element; □, western Alpine element; ●, western European element; ○, eastern Alpine element; ◊, widespread elements; ◆, Carpathian element; Δ, Pyrenean element; ■, south Alpine element; +, noise component.

omitted all species of which there are no closely related species represented in the remaining seven biotic elements. A total of 161 species belonging to 48 species groups remained. A chi-square test showed that closely related species belong significantly (P < 0.00001) more often to the same biotic element than should be expected by chance.

If two species which originated by vicariance disperse across the barrier which separated them and colonize the same area, they will be classified in the same widespread biotic element. Therefore, it is reasonable to exclude elements which occupy areas into which the areas occupied by geographically more restricted elements are nested from the analysis of the distribution of closely related species across biotic elements. In the case of the north-west European land snails the exclusion of the two more widely distributed regional clusters from the analysis did not affect the result that closely related species belong significantly more often to the same biotic element than should be expected by chance.

This result is also neither affected by an exclusion of misclassified species (with a wide range outside the study area) nor by the variations of the cluster solutions which were found with variations of the parameters used for the clustering algorithm (see above).

**Dependence on scale**

It is possible that the vicariance events by which closely related species originated occurred at a smaller spatial scale than can be recognized with the chosen grid (c. 10,000 km² squares). Then, the apparent clustering of such species in
biotic elements might be a result of an artificial lumping of adjacent biotic elements.

To check this source of error, we examined the eastern Alpine element, the element with the highest number of species restricted to less than six 100 km squares (28 species), at a finer spatial scale. We recorded the distribution of the 35 eastern Alpine species in a 20 km grid (c. 400 km² squares; 25 times as fine as the grid used in the main analysis) and repeated the test for clustering of distribution areas. The ratio of the sum of the 25% smallest distances to the sum of the 25% largest distances between the eastern Alpine species is significantly smaller than should be expected \((P < 0.001; \ T = 0.347\) compared with \(0.386 < T < 0.588,\) mean 0.454 for 1000 simulated data sets). Again, the test indicates that there is a clustering of distribution areas. Only one cluster besides the noise component was found with PRABCLUS. This cluster includes species centred in southern Carinthia. The clustering of the species of the eastern Alpine element in Carinthia confirms the result of the analysis based on the 100 km squares (Fig. 2a).

**DISCUSSION**

**Biogeographical tests of the vicariance model**

Other biogeographical tests of the vicariance model proposed so far are based on a comparison of area cladograms of different taxa. If the cladogenesis of the taxa occurring in a region is determined by successive vicariance events, the area cladograms of these taxa should be concordant (Rosen, 1976, 1978; Platnick & Nelson, 1978; Nelson & Platnick, 1981; Wiley, 1981, 1988; Humphries & Parenti, 1999; Green et al., 2002). However, the area cladogram approach neglects the problems in identifying and delimiting areas of endemism. Areas of endemism cannot be delimited with biogeographical data alone, if dispersal occurred (Hausdorf, 2002). Moreover, there are hardly any studies in which it has been tested whether there is really non-random congruence between area cladograms of different taxa. In the protocol proposed above, it is tested first whether the distribution areas are clustered at all. If this is the case, biotic elements, which would be a consequence of a fragmentation of an ancestral biota by vicariance events (Hausdorf, 2002), are determined. Only if at least three biotic elements can be identified and if groups of closely related species are not clustered within elements, but are distributed across elements, it is reasonable to convert taxon cladograms in element cladograms by replacing the names of the taxa by the biotic elements to which they belong (Hausdorf, 2002) and to check whether they are concordant. If the observed degree of matching is not greater than would be expected for independently derived cladograms, there is no need to invoke vicariance (Simberloff, 1987). This test demands extensive phylogenetic analyses of the studied taxa.
The proposed tests do not depend on the assumption that there are areas of endemism in any case and that more or less arbitrarily chosen palaeogeographical or geomorphological units correspond to these areas of endemism. Another advantage of this stepwise test protocol is that extensive phylogenetic analyses are not necessary for the first tests. Thus, the distribution data of many taxa can be used to test whether there is a general pattern, whereas in tests based exclusively on comparison of cladograms only a few taxa for which cladograms are available are considered and it is not tested whether their distribution areas correspond to a more general pattern.

If the tests show that the prediction of the vicariance model are met, the hypothesis that speciation by vicariance was the predominant speciation mode cannot be rejected. If the prediction of the vicariance model are not met, the situation is more complicated. A negative result might indicate that speciation modes other than vicariance were frequent or that distribution patterns which resulted from vicariance events were obscured by extensive post-speciation dispersal. At present it is difficult to distinguish between these alternatives, because we do not have a null model that can simulate dispersal and extinction in a realistic manner so that we could evaluate the real pattern against patterns which might result under different scenarios. In any case the biogeographical data cannot be used to reconstruct the history of the biota and the study area in form of a sequence of vicariance events, if the patterns which are predicted by the vicariance model are not found.

Another biogeographical approach to investigate the relative frequencies of different diversification modes is to examine the spatial relationships and the relative size of distribution areas of sister species and sister clades (Wiley, 1981; Wiley & Mayden, 1985; Lynch, 1989; Chesser & Zink, 1994; Barraclough & Vogler, 2000). This approach has been criticized, because the current distribution of a species is not necessarily a reliable indicator of the range at the time of speciation (Chesser & Zink, 1994; Barraclough & Vogler, 2000; Losos & Glor, 2003). Our approach to test the vicariance model is less sensitive to post-speciation range expansions or contractions, because it does not depend on relative range sizes and because biotic elements can still be recognized even if there is some post-speciation dispersal or extinction (Hausdorf, 2002).

Analysis of the northwest European land snail fauna

The test for clustering of distribution ranges of the northwest European land snail species indicates that the ranges are more clustered than should be expected under the null model. One widespread and seven regional biotic elements could be identified with a cluster analysis. 21% of the species are classified in the noise component, i.e. they cannot be assigned reasonably to any biotic element. This indicates that they originated by speciation modes other than vicariance or that their ranges were extensively modified by post-speciation range shifts.

Widespread elements which occupy regions into which the areas of two or more geographically restricted elements are nested might be the result of an expansion of species which originated in different areas of endemism into other areas of endemism or the lack of a response of some species to vicariance events. For example, the areas occupied by the E-Alpine and the Carpathian element are nested in the area occupied by the eastern Alpine-Carpathian element. The eastern Alpine-Carpathian element might include species which originated in the eastern Alps or the Carpathian Mountains and expanded into the other area afterwards and species which were widespread in the eastern Alpine-Carpathian region before the eastern Alps and the Carpathian Mountains were separated by a vicariance event and which did not respond to that event.

The test of the distribution of closely related species across biotic elements showed that, contrary to the prediction of the vicariance model, closely related species occur significantly more often in the same biotic element than should be expected. This result is neither affected by an exclusion of misclassified species (with a wide range outside the study area) nor by the variations of the cluster solutions which were found with variations of the parameters used for the clustering algorithm. We would expect such a pattern, if other speciation modes, peripatric, parapatric or sympatric speciation, were frequent. However, we cannot exclude the alternative explanation, that the imprint of vicariance on the distribution patterns has been completely obscured by extensive post-speciation dispersal. The possibility that the clustering of closely related species in biotic elements is a consequence of an artificial lumping of adjacent biotic elements as a result of a too coarse grid size has been examined by an analysis of the eastern Alpine element, the element with the highest number of species restricted to less than six 100 km squares, at a finer spatial scale. No more restricted biotic elements were detected in the eastern Alps by the more fine-grained analysis and, thus, there is no reason to suppose that the clustering of closely related species in biotic elements is a consequence of an artificial lumping of adjacent biotic elements.

The results may be partly explained by range shifts that were caused by Pleistocene climatic fluctuations. The core areas of the regionally restricted biotic elements (Pyrenees, western Europe, southern Alps, eastern Alps, Carpathian Mountains; Fig. 2a) correspond well with the centres of sets of nested subsets (Hausdorf & Hennig, 2003a) as well as with supposed glacial refugia of trees (Huntley & Birks, 1983). Glacial refugia north of the Mediterranean peninsula (Iberia, Italy and the Balkans), e.g. at the borders of the Alpine region, have been supposed for many land snails and other invertebrates for a long time (e.g. Poliński, 1928; Zimmermann, 1932; Klemm, 1939, 1974; Holdhaus, 1954; Janetschek, 1956) and there is recent fossil evidence for such refugia (Willis et al., 2000). The core areas of the regionally restricted biotic elements might indicate the positions of such ‘cryptic northern refugia’ (in the sense of Stewart & Lister, 2001) of land snails, especially of forest dwelling species, which could
not survive in the tundra-steppe belt between the North European and the Alpine ice sheets.

The importance of the core areas of the biotic elements as refugia is also supported by the fossil record. In former, warmer interglacials some species which are more or less restricted to these areas at present [e.g. the Pyrenean Neniatlanta pauli (Mabille), the S-Alpine Drepanostoma nautiliiforme Porro, the eastern Alpine Macrogastria densestriata (Rossmaßler), Fusulus interruptus (C. Pfeiffer) and Aegopinella ressmanni (Westerlund), the Carpathian Perforatella dibothriion (Kimakowicz), Faustina rossmaessleri (L. Pfeiffer) and Drobacia banatica (Rossmaßler) were more widespread in Central Europe (e.g. Lożek, 1964). At some Central European localities species currently endemic to different core areas occurred sympatrically (sometimes even with species currently restricted to North and Central Asia and Caucasus, e.g. Gastrocopta theeli (Westerlund); Lożek, 1964). This dynamic mixing of different biotic elements contradicts the model proposed by Riddle (1996) which suggests that range-shifting does not breach the barriers between areas of endemism, i.e. that biotic elements do not intermingle. Similar cases are known from beetles (Coope, 1990).

However, the core areas of the biotic elements were not only refugia. In these areas several groups radiated [e.g. Cochlostoma (Obscurella), Abida and Chondrina in the Pyrenees, Orcula in the eastern Alps, Vestia and Faustina in the Carpathians], of which most species never dispersed into Central and northern Europe. Some of these radiations might be rather recent and we can suppose that the ranges of vicariating endemic species which are partly restricted to small areas are not strongly modified by post-speciationsal dispersal and/or regional extinction. Nevertheless, we do not find separate clusters of ranges within these areas, even, if they are examined at a higher resolution, as we have done for the eastern Alps. This might indicate that these radiations were not the result of an ordered sequence of vicariance events, but that other speciation modes were predominant. Data on the relative ages of the examined taxa might contribute to the clarification of this issue in the future.

If the distribution patterns of organisms with low vagility like land snails do not correspond with the predictions of the vicariance model, it is even less likely that vicariance does shape distribution patterns in more mobile taxa like birds.

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