

Phylogenetic analysis of the latitude-niche breadth hypothesis in the butterfly subfamily Nymphalinae

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Abstract. 1. One possible explanation for the latitudinal gradient in species richness often demonstrated is a related gradient in niche breadth, which may allow for denser species packing in the more stable environments at low latitudes.

2. The evidence for such a gradient is, however, ambiguous, and the results have varied as much as the methods. Several studies have considered the non-independence of species, but few have performed explicit phylogenetic analyses.

3. In the present study, we tested for a correlation between diet breadth and latitude of distribution in Nymphalinae butterflies using generalised estimating equations (GEE) and accounting for phylogenetic independence.

4. Using a simple model with only latitude of distribution as a predictor variable revealed a significant positive relationship with diet breadth. Previous studies, however, have shown that diet breadth is also correlated with butterfly range size, and in turn, that range size may be correlated with latitude of distribution. Including geographical range size in the model also turned out to have a profound effect on the results – to the extent that the relationship between latitude of distribution and diet breadth was effectively reversed.

5. We conclude that, at least for this group of butterflies, there is no evidence for a positive correlation between latitude of species distribution and diet breadth when controlling for range size, and that the effect may actually even be reversed.

Key words. Diversification, generalisation, host range, latitude, polyphagy, specialisation.

Introduction

One of the basic patterns of biodiversity is the latitudinal gradient of increasing species richness from the polar regions towards the equator. Although there are exceptions (such as penguins, seals, and some parasites), this pattern holds true for a wide range of groups, including trees, mammals, and invertebrates, on land as well as in freshwater and marine environments (Willig *et al.*, 2003). Understanding the cause of such a general pattern may be an important step in understanding sources of diversity. A number of possible reasons for this latitudinal diversity gradient have been proposed, such as predation, productivity, and climate (Rohde, 1992; Hawkins *et al.*, 2003). Another possibility is that the latitudinal gradient in diversity is related to niche breadth (MacArthur &

Levins, 1967). The latitude-niche breadth hypothesis suggests that a latitudinal difference in environmental stability can cause differences in niche breadth, which in turn can result in a latitudinal diversity gradient.

According to the hypothesis, a species niche breadth is likely to reflect the stability of the environment in which it lives. Unpredictable environments, such as seasonal climates, where the availability of resources varies in time and space, will favour wider niches over more specialised resource use. This is because a generalist can use different resources as the availability varies, whereas, the specialist is dependent on the availability of one or a few resources. A stable environment, on the other hand, should favour narrower niches, as a specialist with more efficient resource use will do better in competition with other organisms in the community. In turn, niche breadth may determine how tightly species can pack, because competition limits the number of similar species that can coexist. If niches are narrow, more species can coexist for a given resource. Therefore, assuming that the environment is more

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stable in the tropics than in temperate areas, we should expect species to be more specialised and more densely packed in the tropics, thereby explaining the greater diversity in the tropics.

If variation in environmental stability and niche breadth is responsible for the latitudinal gradient in diversity, these characteristics must themselves vary along a latitudinal gradient. The tropics are often considered to be more stable, although very few studies have investigated latitudinal gradients in environmental stability. Vázquez and Stevens (2004) looked at the variation in temperature and precipitation with latitude and found that variation in temperature increases with increasing latitude as expected, whereas, precipitation shows the opposite pattern. In order to determine which is more relevant it is necessary to investigate which aspect of the environment is more important in determining niche breadth for each species. More studies have investigated whether niche breadth varies with the latitude of the species distribution. These studies have also produced inconclusive results, some finding a positive correlation between niche breadth and latitude of distribution (Scriber, 1973; Pagel *et al.*, 1991; Loder *et al.*, 1998; Eeley & Foley, 1999; Dyer *et al.*, 2007; Krasnov *et al.*, 2008), while others have found no significant correlations (Fiedler, 1997; Ollerton & Cranmer, 2002; Novotny *et al.*, 2006) or even negative ones (Beaver, 1979). Meta-analysis by Vázquez and Stevens (2004) suggests that there is no overall support for the hypothesis, although the small number of studies included might mean that the effect is lost. A possible reason for the varying results may be that the studies differ in their definition of niche breadth, measure of latitude of distribution and geographical and taxonomic scope.

Most studies have defined niche breadth as the range of hosts/prey used, whereas, others have looked at the habitat types occupied. The use of diet breadth as a measure of niche breadth in, for example, butterflies and parasites can be justified by the fact that they spend a substantial part of their life on the host (Scriber, 1973). On the other hand, there are a variety of ways to measure diet breadth, and results may vary depending on whether the number of host taxa, proportion of specialists or the taxonomic diversity is used. Moreover, results are hard to compare because of differences in scale, ranging from local to global, and the variety of latitudinal measures used. These measures have included comparisons of tropical and temperate forests, latitudinal bands, and the mean latitude of the species distribution.

The most important methodological difference is perhaps whether comparisons are made between communities or within a taxonomic group. The former restricts sampling geographically by looking at the specificity of the species found in the communities, whereas, using the latter, sampling is restricted to a taxonomic group and analysed throughout its latitudinal range. Studies performed at the community level have the advantage of wider taxonomic coverage, however, the mechanisms behind a potential difference are less clear. They could result from diet breadth evolution in direct response to a shift in latitudinal distribution, but also from sorting of species with different diet breadths or by different speciation rates. Comparisons within a taxonomic group, on the other hand, determine if species evolve a more specialised or generalised diet breadth

as a response to shifts in the latitudinal range of their distribution. Several taxonomic groups have been investigated for a correlation between niche breadth and latitude of distribution. However, very few of these have accounted for phylogeny (see Krasnov *et al.*, 2008).

Here we investigate a possible correlation between latitude of distribution and diet breadth for the Nymphalinae subfamily using phylogenetic analyses. The Nymphalinae butterflies are suitable for this type of study as they are distributed throughout the world at a wide range of latitudes, and range from highly host specific to very polyphagous. It has also been shown that host use is very dynamic within this group, with evidence for evolution of diet breadth towards both narrower and broader repertoires (Janz *et al.*, 2001).

Materials and methods

For the purpose of the present study we used the diverse butterfly subfamily Nymphalinae containing 496 species in 56 genera (see Wahlberg *et al.*, 2005). The 182 species (in 36 genera) used in this study are relatively well known with data available for diet breadth and distribution. The phylogenetic analyses were performed on a subset of 144 species (in 35 genera) for which sequence data are available from previous studies (Wahlberg & Zimmermann, 2000; Zimmermann *et al.*, 2000; Wahlberg *et al.*, 2003, 2005, 2009a,b; Kodandaramaiah & Wahlberg, 2007; Wahlberg & Freitas, 2007; Leneveu *et al.*, 2009).

Phylogeny

Sequence data from three gene regions were included: the COI (Cytochrome Oxidase subunit I), EL-1 α (Elongation Factor 1 alpha) and *wingless*, these are available on Genbank (for accession numbers see Appendix S1). Sequences were downloaded and aligned in BioEdit v7.0.5.3 (Hall, 1999). The alignment was straightforward.

The fit of different nucleotide substitution models was estimated based on likelihood scores calculated in PAUP* 4.0 (Swofford, 2001) analysed on the ModelTest server 1.0 (Posada, 2006) running ModelTest 3.8 (Posada & Crandall, 1998) using the standard AIC (Akaike Information Criterion) and using branch lengths as parameters. The suggested model, GTR + I + G, was imposed on the three gene partitions separately and Maximum likelihood (ML) analysis was conducted using RAxML 7.0.4 (Stamatakis *et al.*, 2008) via the Cyberinfrastructure for Phylogenetic Research (Cipres) Portal v.1.15 (Miller *et al.*, 2009) using the default parameters. Bootstrap values were calculated from 1000 pseudo-replicates.

Diet breadth and latitude data

Host plant data were collected from the literature for each butterfly species (Scott, 1986; DeVries, 1987; Corbet, 1992; Larsen, 1992, 2005; Smith *et al.*, 1994; Igarashi & Fukuda, 1997; Parsons, 1998; Braby, 2000; Janz *et al.*, 2001;

Wahlberg, 2001; Tennent, 2002; Savela, 2007). Where species and subspecies status differed between diet breadth data and distribution data, we followed the nomenclature used for the distribution data.

As host records at the level of plant species are often uncertain or lacking, the data were collected at the genus level. Also, in order to avoid anecdotal records, we took the same steps used by Janz and Nylin (1998) and Janz *et al.* (2006), where records were only included if: (i) several plant genera are reported in a family, (ii) several species are reported in a plant genus, (iii) the genus is used by other butterflies in the genus, or (iv) there are several independent sources. Observations made in the laboratory were not included, because laboratory data are not available for many butterfly species and host plants, also these may not reflect the actual diet breadth in the field (Janz *et al.*, 2001). Two measures of diet breadth were used. The first measure was the number of genera used. The second measure was designed to reflect the greater host diversity of butterflies that feed on plants not only in several genera but also several families or even orders. For this reason the plant genera were assigned to family and order according to Stevens (2001) and the number of families and orders were then multiplied with the number of genera to create an index of diet breadth.

Latitude of distribution was measured as the centroid, that is the geometric centre, of each species distribution. Automatically digitised distribution maps were collected from Savela (2007), and the accuracy was checked against available distribution maps in the literature (Scott, 1986; Igarashi & Fukuda, 1997; Braby, 2000) and adjusted if necessary. To avoid latitudinal distortion as a result of maps not being in an equal area projection, the downloaded maps were used to create selections in a GIS (ArcMap 9.2) on the world map that is distributed with the software. The centroid latitude for each species distribution was then calculated using a VBA script in the Field Calculator. The absolute latitudes were used, making no difference between northern and southern hemispheres. Latitude of distribution data were used in two ways so as to make results more comparable to previous studies: as a continuous character and as a categorical character (tropical/temperate). The continuous data were converted to binary data by categorising all distributions with a centroid latitude below 23.5° as tropical and distributions with centroids above 23.5° as temperate.

Analyses

To test if species are independent of each other with respect to diet breadth and latitude of distribution, lambda was estimated implementing Continuous, and Maximum likelihood in BayesTraits v1.0 (Pagel, 1999; Pagel & Meade, 2006). Lambda measures if phylogeny correctly predicts the patterns of covariance among species on a given trait. Lambda was estimated for latitude of distribution and both diet breadth measures. These analyses indicated a significant phylogenetic signal (see Results) suggesting that phylogeny should be taken into account when studying latitude of distribution and diet breadth.

Latitude of distribution and diet breadth were then analysed phylogenetically to test for a correlation, under the assumption

that related species are more similar than expected by chance. This was done using generalised estimating equations (GEE), as implemented in the APE package (Paradis & Claude, 2002; Paradis *et al.*, 2004) in R 2.9.2 (R Development Core Team, 2009). This method incorporates species relatedness as a correlation matrix and uses a generalised linear model approach, allowing data to be analysed using non-normal response variables. The data (highly skewed, positive, and continuous) suggested using the gamma family and log link would be appropriate. Branch lengths for the phylogeny were proportional to the number of changes along each branch. Furthermore, we corrected for range size as this has previously been shown to correlate with both diet breadth and latitude of distribution (Krasnov *et al.*, 2008).

In order to test the robustness of the results, we performed a series of diagnostic tests. First, because both range size and diet breadth data are highly skewed, we re-analysed the data having removed outliers in range size and diet breadth respectively to check for undue influence. Furthermore, to test whether the correlation was caused by a disproportionate effect within or between the tropical and temperate regions, we categorised the data into a binary variable. This variable was then used as a predictor variable for the whole data set, but also to analyse the data separately for the temperate and tropical areas.

Results

The raw data, showing how diet breadth (number of genera) varies with latitude of distribution, can be seen in Fig. 1. However, results from the test of phylogenetic signal showed that both diet breadth measures received intermediate lambda estimates (0.48 for diet breadth index and 0.45 for number of genera), indicating that there was some effect of phylogeny. Latitude of distribution, on the other hand, showed a stronger phylogenetic signal ($\lambda = 0.99$). The intermediate values of diet

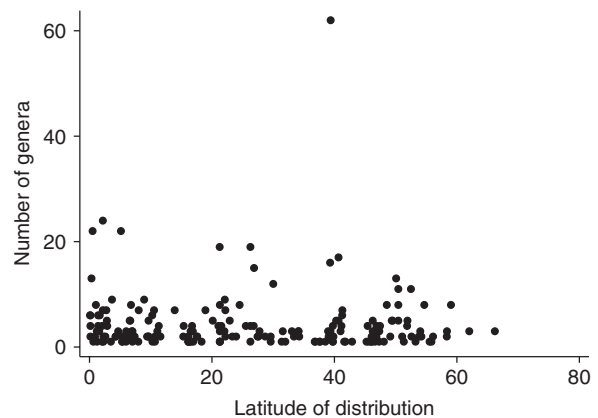


Fig. 1. The relationship between the number of host plant genera and the absolute value of the latitude of distribution for 182 Nymphalinae species. The outlier is *Vanessa cardui*. The data for number of host genera is highly skewed with most species only feeding on a few host plants, therefore, these data were analysed phylogenetically using Generalised Estimating Equations which allows non-normal response variables.

Table 1. Results for the phylogenetic analysis using GEE, for the whole data set and including latitude of distribution as a continuous variable.

| Diet breadth measure | Variable | dfp* | Estimate | S.E. | p-value |
|----------------------|------------|--------|------------------------|-----------------------|------------------|
| <i>Model 1</i> | | | | | |
| Diet breadth index | Latitude | 39.870 | 0.039 | 0.010 | <0.001 |
| Number of genera | Latitude | 39.870 | 0.011 | 0.005 | 0.021 |
| <i>Model 2</i> | | | | | |
| Diet breadth index | Latitude | 39.870 | -5.30×10^{-2} | 8.78×10^{-3} | <0.001 |
| | Range size | | 5.39×10^{-8} | 5.01×10^{-9} | <0.001 |
| Number of genera | Latitude | 39.870 | -7.02×10^{-3} | 3.46×10^{-3} | 0.050 |
| | Range size | | 2.05×10^{-8} | 1.98×10^{-9} | <0.001 |

*Phylogenetic degrees of freedom (Paradis & Claude, 2002).

Model 1 shows the results for the simplest model including latitude of distribution as the only predictor variable. Model 2 shows the results when range size is included in the model. Significant p-values are in bold.

breadth and high lambda values for latitude of distribution suggested that data should be analysed phylogenetically. The phylogeny constructed for these analyses was well supported and largely consistent with previously published Nymphalinae phylogenies (e.g. Wahlberg *et al.*, 2005).

In the simple model with latitude of distribution as the sole predictor variable there was a significant positive effect on diet breadth, suggesting that species at higher latitudes have larger diet breadth than species at lower latitudes. This result was consistent for the measure of diet breadth used (Table 1: Model 1). However, when range size was included in the model it had a significant effect on the correlation between latitude of distribution and diet breadth. Indeed, when the confounding effect of range size was controlled for, the relationship between diet breadth and latitude of distribution was reversed, now showing a significant negative correlation. This suggests that for a given range size species at higher latitudes have smaller diet breadth than species at lower latitudes. This result was also consistent for the different diet breadth measures (Table 1: Model 2).

The negative correlation remained when range size outliers were removed; this was also true for outliers in the diet breadth index (Table 2). If the whole data set was analysed with latitude of distribution treated as a binary character (tropical/temperate) the result differed between diet breadth measures; when using the diet breadth index the negative correlation remained, but when using genera it was significantly positive. When the data were analysed for the tropical and temperate regions separately, the negative correlation remained significant for the temperate areas, but for the tropical data it was not significant. Taken together, these results indicate that the correlation is fairly robust, but to some degree, dependent on how the data are analysed.

Discussion

Most previous studies of the latitude-niche breadth hypothesis have not considered phylogeny. The present study shows that related species are non-independent with respect to latitude of distribution and diet breadth, thereby necessitating the incorporation of phylogeny (Felsenstein, 1985). Even so, the simplest model, using latitude of distribution as the sole predictor variable, showed a positive correlation between latitude of distribution and diet breadth (Table 1: Model 1), which is in accordance with several previous studies (Scriber, 1973; Pagel *et al.*, 1991; Loder *et al.*, 1998; Eeley & Foley, 1999; Dyer *et al.*, 2007; Krasnov *et al.*, 2008).

Including range size in the model, however, caused a reversal of the pattern so that latitude of distribution now showed a significant negative correlation with diet breadth (Table 1: Model 2). Including range size in the model is justified because range size has previously been shown to correlate with diet breadth on the species level (Slove and Janz, unpublished), where species with wider diet breadths also have larger range sizes. In addition, range size may be larger at higher latitudes as suggested by Rapoport's rule, although support for this varies (Stevens, 1989; Rohde, 1999; Ruggiero & Wrenkraut, 2007).

Our analysis supported Rapoport's rule and showed that the narrower diet breadths at lower latitudes can be explained by

Table 2. Results for the diagnostic analyses, performed to test the robustness of Model 2 (which includes range size) in Table 1.

| Type of diagnostics | Diet breadth measure | Variable | dfp* | Estimate | S.E. | p-value |
|----------------------------------|----------------------|------------|--------|------------------------|-----------------------|------------------|
| Latitude as binary variable | Diet breadth index | Latitude | 39.870 | -8.05×10^{-1} | 2.50×10^{-1} | 0.003 |
| | | Range size | | 3.90×10^{-8} | 3.84×10^{-9} | <0.001 |
| Latitude as binary variable | Number of genera | Latitude | 39.870 | 2.80×10^{-1} | 1.22×10^{-1} | 0.028 |
| | | Range size | | 1.78×10^{-8} | 1.88×10^{-9} | <0.001 |
| Excl diet breadth index outliers | Diet breadth index | Latitude | 39.802 | -7.27×10^{-2} | 1.45×10^{-2} | <0.001 |
| | | Range size | | 1.02×10^{-7} | 1.09×10^{-8} | <0.001 |
| Excl range size outliers | Diet breadth index | Latitude | 35.866 | -7.90×10^{-2} | 1.73×10^{-2} | <0.001 |
| | | Range size | | 1.66×10^{-7} | 3.29×10^{-8} | <0.001 |
| Tropical only | Diet breadth index | Latitude | 23.744 | -4.40×10^{-2} | 2.65×10^{-2} | 0.112 |
| | | Range size | | 6.50×10^{-9} | 1.58×10^{-8} | 0.684 |
| Temperate only | Diet breadth index | Latitude | 19.279 | -7.23×10^{-2} | 2.40×10^{-2} | 0.008 |
| | | Range size | | 9.60×10^{-8} | 1.12×10^{-8} | <0.001 |

*Phylogenetic degrees of freedom (Paradis & Claude, 2002).

Analysed using GEE and accounting for phylogeny. Significant p-values are in bold.

the fact that range size varies with latitude, thus confounding the effect of latitude itself. When controlling for range size, the remaining effect of latitude of distribution was actually reversed, suggesting that narrower diet breadths at lower latitudes is mostly a consequence of smaller range sizes. This is not the first time a negative correlation has been found for diet breadth and latitude of distribution; a similar pattern was shown in Scolytidae and Platypodidae (Beaver, 1979). Beaver suggested that a reason for this pattern could be that even if tropical communities may be more temporally stable, they are often spatially very heterogeneous, making any specific plant species more difficult to localise. This would then favour the inclusion and/or maintenance of multiple hosts in the repertoire (Beaver, 1979).

Tropical plant communities are also typically more diverse, but it is not intuitively clear how such a difference in plant diversity should be connected to the diet breadth of butterflies feeding on them. One possibility is that the multitude of different resources available should be associated with increased specialisation, but it is also possible – analogous to Beaver's (1979) reasoning on spatial heterogeneity above – that increased plant diversity would make any specific plant more difficult to localise, which would then favour generalisation. This is a complex and interesting question that merits further investigation. It is also worth noting that actual diet breadth of local populations may often be narrower than the species-level diet breadth (Fox & Morrow, 1981; Thompson, 1994), either because of local adaptation or plasticity. Such local differences would be more pronounced in species with wide geographical ranges and would tend to reduce the effect of niche width on species packing.

We performed several explorative diagnostic analyses to test the robustness of the results. Removal of range size outliers and diet breadth outliers did not affect the results significantly, however, treating latitude of distribution as a categorical variable yielded varying results depending on which diet breadth measure was used (Table 2). Also analysing tropical and temperate regions separately suggests that the result may be dependent on a strong effect of latitude of distribution on diet breadth in the temperate regions.

In other words, the results are somewhat dependent on how data are analysed. Just as previous studies have received varying results depending on the methods used, results presented here similarly show that the result (positive, negative or no correlation) is dependent on the model used and how latitude of distribution and diet breadth is measured. Host plant and distribution data underlying the analysis are sometimes uncertain, and it is also possible that such errors could affect the analysis. This is of particular concern if there is reason to believe that there is a systematic bias. Although butterflies are comparatively well documented – with extensive data from all parts of the world – it is still possible that more is generally known about temperate than tropical species. This would tend to underestimate the diet breadths of tropical species, making them seem more specialised than they really are, and thus increase the likelihood of finding a positive correlation with latitude of distribution.

A similar underestimation of range sizes of tropical species could mean that the effect of range size on the relationship between diet breadth and latitude of distribution is overestimated. If the effect of range size is actually considerably weaker or even non-existent this could mean that the true relationship is positive. However, because of the way geographical distributions are reported in the literature, where even one single record will be extrapolated into the whole region where it is located, incomplete sampling in the tropics would actually overestimate range sizes and latitudinal ranges more often than it would underestimate them. Hence, if indeed data from tropical regions are less comprehensive, we argue that this would actually increase the likelihood of finding a positive correlation between diet breadth and latitude of distribution.

Nymphalinae is a geographically widespread group that probably started to diversify around the K/T boundary around 65 million years ago (Wahlberg, 2006). During this time, species in the group have repeatedly undergone changes in diet breadth, as well as latitudinal range, resulting in a geographically widespread subfamily with diverse host plant associations. This makes it possible to explicitly analyse changes in these characters. Consequently, we can conclude that at least in this group of butterflies diet breadth is not more specialised in the tropics than in temperate areas. If anything the pattern is reversed.

The mixed results of this and previous studies suggest that there is no general pattern of increasing niche breadth with increasing latitude of distribution. It is, however, possible that the pattern is group-specific, and Vázquez and Stevens (2004) suggested a mechanism by which such a latitudinal gradient could arise in some groups but not others. On the other hand, the lack of general pattern for niche breadth and latitude of distribution would mean that it is unlikely to be the explanation for the more general pattern of increasing species richness with decreasing latitude of distribution.

Acknowledgements

We wish to thank Niklas Wahlberg and Ullasa Kodandaramaiah for help with the phylogeny. The manuscript was improved by comments of Ian Henshaw. This work was supported by grants from the Swedish National Science Research Council and the Stockholm University Faculty of Science to NJ.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference:

DOI: 10.1111/j.1365-2311.2010.01238.x

Appendix S1. List of taxa used in this study with their Genbank accession numbers.

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Accepted 29 July 2010