Research

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Phylogenetic alpha and beta diversities of butterfly communities correlate with climate in the western Swiss Alps

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The observation of non-random phylogenetic distribution of traits in communities provides evidence for niche-based community assembly. Environment may influence the phylogenetic structure of communities because traits determining how species respond to prevailing conditions can be phylogenetically conserved. In this study, we investigate the variation of butterfly species richness and of phylogenetic α- and β-diversities along temperature and plant species richness gradients. Our study indicates that butterfly richness is independently positively correlated to temperature and plant species richness in the study area. However, the variation of phylogenetic α- and β-diversities is only correlated to temperature. The significant phylogenetic clustering at high elevation suggests that cold temperature filters butterfly lineages, leading to communities mostly composed of closely related species adapted to those climatic conditions. These results suggest that in colder and more severe conditions at high elevations deterministic processes and not purely stochastic events drive the assemblage of butterfly communities.

Whether species assemblages are governed by stochastic or deterministic processes is a central question to understand the determinants of species distributions, but also to predict community response to global changes (Wiens et al. 2010). While the niche theory stipulates that factors such as competition or environmental filtering should play a major role in determining local species assemblages, the neutral theory emphasized the role of stochastic events (e.g. dispersal, local extinction) in community assembly (Grime 1977, Hubbell 2001, Chave 2004). Chase (2007) demonstrated that the balance between deterministic and stochastic processes in governing species assemblages is influenced by prevailing environmental conditions. Deterministic, niche-based processes are expected to be strong drivers of community structure in harsh environments while more benign environmental conditions may be dominated by stochastic processes. Since traits inherited through the evolutionary history of lineages define the capacity of species to persist within communities in a given environment, these traits also influence the phylogenetic community structure (Graham et al. 2009). Examining how species belonging to the same assemblage are distributed in phylogenies may shed light on the processes that govern communities' assembly.

Understanding how the phylogenetic structures observed in communities differ from those of random assemblages may provide information on the mechanisms underlying community assembly (Cavender-Bares et al. 2009). Traditionally, functional traits have been used to understand community structure (de Bello et al. 2009). They are considered to provide valuable information about a species' ecological niche because they arose in a given environment, associated with particular selective pressures. Useful traits may also arise under different conditions and represent exaptation ecologically fitted to the current environment (Gould and Vrba 1982). It is predicted that traits will be clustered – i.e. traits will be more similar across the species in a community than those randomly drawn from the regional trait pool – if they confer the ability to tolerate particular environmental conditions. This phenomenon is known as 'environmental filtering'. In contrast, trait divergence – i.e. phenotypic traits within a community are less similar than expected under a random assembly process – is expected when competition mediates community assembly, a phenomenon known as 'limiting similarity'. This is because species sharing similar traits are expected to compete for similar resources (Weiher and Keddy 1995), whereas species with different functional attributes are expected to use different resources (i.e. resource partitioning; MacArthur and Levins 1967). However, the measured traits are not necessarily as 'functional' as theoretically expected and may not be the ones affecting the species' response to particular environmental heterogeneity. As a result, the assumption of a relationship between a phenotypic traits and the structure

of a communities can prove difficult to test in some instances (Cavender-Bares et al. 2009). When this is the case, an analysis that considers phylogenetic relatedness may help addressing this issue in a way complementing trait-based approaches. Investigating the phylogenetic diversity, especially in terms of phylogenetic clustering and overdispersion, can thus provide useful additional insights into the ecological and evolutionary factors shaping communities (Webb et al. 2002). However, phylogenetic trait conservatism may not always be the rule and high trait lability may also be observed in regional species pools (Losos et al. 2003, Cavender-Bares et al. 2004).

The relative effects of the environment on trait and phylogenetic diversity as drivers of community assembly have traditionally been assessed within communities, but only rarely between communities (de Bello et al. 2009). In contrast, regional phylogenetic diversity is known to result from phylogenetic diversity values present both within (α diversity) and between (β diversity) communities (Graham and Fine 2008). At the landscape scale, environmental conditions can influence not only α but also the β diversity of communities. As a consequence, investigating the variation of both α and β components of phylogenetic diversity across a heterogeneous landscape can yield additional important information for understanding the drivers of local community assembly.

Only a few studies have examined changes in phylogenetic diversity along environmental gradients. Elevation gradients provide the opportunity to analyse geographically close communities experiencing extremely contrasted environmental conditions. Machac et al. (2010) studied patterns along an elevation gradient, documenting a contrasting pattern of overdispersion – suggesting competition – in ant communities at higher temperatures, and clustering at lower temperatures, suggesting environmental filtering. Similarly, Graham et al. (2009) and Pellissier et al. (2012c, in press) found that hummingbird and bumblebee communities respectively tended to be phylogenetically clustered at high elevations and overdispersed at low elevations. Furthermore, in their study involving several taxa, Bryant et al. (2008) found that microbial communities were phylogenetically clustered over all elevations, whereas plants tended to be increasingly phylogenetically overdispersed at higher elevations.

Butterflies interact with several groups of organisms in antinomic ways (i.e. they feed on plants as larvae and act as pollinators during adulthood) and are therefore important agents of ecosystem processes. As indicated by the frequent use of butterflies as bioindicators, understanding community structuring within this taxon can increase our knowledge about environmental influence on entire ecosystems. It has been demonstrated that climatic features**,** in particular temperature and moisture, have a determining influence on the composition of butterfly communities (Stefanescu 2004, Menéndez et al. 2007, Illián et al. 2010, Stefanescu et al. 2011). Biotic interactions such as competition may also influence community structure. Only few studies addressed this question (Janzen 1973, Gilbert and Singer 1975, Kunte 2008) and even if butterflies appear to exhibit little interspecific resource competition and or limitation, competition may still occur. In contrast, the trophic dependency of butterfly species on plant clades in highly coevolved and specialised systems (Ehrlich and Raven 1964) is expected to have a strong effect on species assemblages in this group.

In this study, we aim to identify some of the factors controlling butterfly species assemblages. For this, we sampled butterfly communities spanning diverse environments in the western Swiss Alps. We investigated variation in phylogenetic α and β diversities along gradients of temperature and plant species richness. The two factors are likely to cause filtering effects. First, the abiotic factor of temperature may affect the survival and development of butterflies (Boggs and Murphy 1997). Second, the biotic factor of plant species richness may control butterfly communities as butterfly species frequently display restricted host-plant ranges (Ehrlich and Raven 1964, Pellissier et al. 2012b) causing a positive correlation between plant species and butterfly species richness, particularly at the local scale (Menéndez et al. 2007). We investigated the following hypotheses: 1) both abiotic and biotic factors should influence the butterfly species richness in communities. Butterfly species richness should be higher in plant rich grassland providing diverse resources and in milder climate. 2) At high elevations climate filters species with respect to their ability to tolerate colder conditions and only a restricted number of lineages should be able to occur causing a lower phylogenetic α diversity. 3) At lower elevations, climate might not have such a large effect on lineages, but competition may influence the phylogenetic α diversity and lead to phylogenetic overdispersion. 4) Abiotic and biotic factors should cause non-random phylogenetic turnover among communities and therefore affect the butterfly phylogenetic β diversity.

Material and methods

Study area and field sampling

The study area is located in the western Swiss Alps (Fig. 1). Elevations in the study area range from 1000 to 3210 m a.s.l. The highlands in this region are occupied by alpine meadows and glaciers, but land use is intense and diversified at lower elevations, with open areas intensively used for agriculture and cattle. Areas of low economic importance generally harbour species-rich grasslands, although the extent of these grasslands has decreased over the last three decades. Land use is limited in areas above the tree line, where grazing by cattle is only possible during summer months. Site selection was conducted following a balanced stratified random sampling design based on elevation, slope and aspect, and considering only regions outside of forested areas (Hirzel and Guisan 2002). Between May and September of 2009 and 2010, 192 sites were sampled. Sixty sites were visited in 2009 and 132 in 2010, by ten entomologists. Each site was visited every three weeks during the vegetation growing season (between three and five visits per site). At the beginning of the field season, sites at the highest elevations were still covered with snow and were sampled as soon as they were snow-free. Following Pollard and Yates (1993), sites were visited during hours of high butterfly activity (10:00–17:00) and

Figure 1. Study area in the western Swiss Alps (black zone in the caption). Black circles show sampled locations. Circle size is proportional to the number of butterfly species found in each location.

only under good weather conditions (i.e. little wind, sunshine and high temperatures). Each site was sampled for 45 min, during which butterflies belonging to the Papilionoidea super-family (sensu Heikkilä et al. 2012, i.e. comprising Hesperiidae) were sampled in a 50×50 m plot. Butterflies were net-captured and identified in situ. The species captured during all visits to a site were pooled in order to approximate the observed communities at that site. Vegetation was exhaustively inventoried in a 4-m^2 subplot at the centre of each plot (for details, refer to Dubuis et al. 2011). A 4-m^2 subplot is representative of the vegetation in larger surfaces (Supplementary material Appendix 1, Fig. A1).

Environmental variables and butterfly richness

Two environmental variables were used in this study: degree-days above 0°C (DDEG) and plant species richness (PLRI). Following the method of Zimmermann and Kienast (1999), degree-days were calculated using a digital elevation model at a 100-m resolution along with meteorological station data. Degree-days are relevant for a caterpillar's ability to emerge as an imago (Boggs and Murphy 1997). Note that in the study area, degree-days are negatively correlated with precipitation. Once calculated, the values of degree-days were extracted for each site. Plant species richness at each site was calculated as the sum of all plant species inventoried. Even if plant richness generally decreases with temperature, at comparable temperatures, plant species richness can also differ among grassland types at different elevations (Dubuis et al. 2011).

Degree-days is likely to influence plant species richness and butterfly species richness (i.e. the number of species found at each site), while plant species richness influences butterfly species richness independently of temperature. To deal with this issue of collinearity, we first related the butterfly species richness to degree days with a linear model. Second, we related the residuals of this first relationship to plant species richness. We tested the significance using permutations as implemented in the lmPerm R package (Wheeler 2010).

Sequence treatment and phylogenetic inferences

Phylogenetic relationships were inferred using DNA sequences for all but one of the butterfly species sampled (Supplementary material Appendix 2, Table A1). Five Thyrididae and two Callidulidae species were included as outgroups (Supplementary material Appendix 2, Table A1). Sequences were obtained from GenBank and included two nuclear markers (EF1-alpha, Wgl) and four mitochondrial markers (16s rRNA, COI, NDH1, NDH5). Sequences were aligned in BioEdit (Hall 1999) using MAFFT (Katoh and Toh 2008), which provided a final concatenated matrix of 4310 base pairs. Reconstructions were conducted using three approaches: a maximum likelihood (ML) and two Bayesian methods (i.e. ultrametric, yielding to a chronogram, and non-ultrametric, resulting in a simple phylogram).

ML searches were performed using RaxML 7.2.6 (Stamatakis et al. 2008), with 10 000 rapid bootstrap analyses followed by a search of the best-scoring ML tree. The analysis was run partitioned, considering a general time-reversible (GTR; Tavaré 1986) model of evolution for all partitions. Analyses were conducted using computational resources available through the NSF CIPRES (Cyberinfrastructure for Phylogenetic Research) portal (San Diego, CA, USA).

MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003) was used to perform Bayesian analyses on the data. Models of sequence evolution for each region were calculated using MrModeltest 1.0 (Nylander 2004) and were chosen based on the Akaike information criterion (AIC). The best AIC score for all partitions was the GTR model that accounted for a gamma distribution in considering rate heterogeneity among sites and allowed for a proportion of invariable sites. Two independent Metropolis-coupled Markov chains (MCMC) starting at different random trees were run for 10 million generations, sampling one tree every 1000 generations. Convergence was accepted when standard deviations reached values of less than 0.01 and when the potential scale reduction factor index (Gelman and Rubin 1992) approached 1.0. We considered the MCMC sampling sufficient when the effective sampling size (ESS) was higher than 200 (verified using Tracer ver. 1.4; Rambaut and Drummond 2004). A burn-in of 1500 sampled generations

was applied, and an all-compatible tree (i.e. one that followed the extended majority rule criterion) was reconstructed using the remaining 8501 trees of each run (a total of 17 002 trees for the two runs), after which Bayesian posterior probabilities (BPP) were calculated.

BEAST ver. 1.6.1 (Drummond and Rambaud 2007) was used to infer phylogenies in a Bayesian ultrametric approach (i.e. to establish a chronogram). In order to perform this analysis, the inference was calibrated using fossil data. Five nodes were thus constrained based on dates estimated by previous studies or on the fossil register, following the approach proposed by Espíndola et al. (2010). Based on the estimations of Heikkilä et al. (2012), the most recent common ancestor (MRCA) to all Papilionoidea was dated to 110 Mya (+/− 10 My). The MRCA of Papilionidae and Lycaenidae were fixed to 48.6 My (+/− 5 My) based on fossil registers from the Eocene (54.8–33.7 Mya; Durden and Rose 1978). The MRCA of families Pieridae and Nymphalidae were fixed to 37.2 Mya (+/− 5 My), based on fossil data from the Priabonian age (37–33.7 Mya; Brown 1976). All priors for fossils had a normal distribution, and the tree prior was set to follow a Yule speciation model. Three independent searches were run for 50 000 000 generations, sampling parameters every 1000 trees. After checking for convergence in Tracer 1.4, a burnin of 20 000 trees was applied and a maximum credibility tree was constructed combining the results of all converged runs (90 000 trees) using LogCombiner 1.6.1 and TreeAnnotator 1.6.1 (Drummond and Rambaud 2007). The similarity between the inferences obtained using the three phylogenetic approaches was quantified by calculating the quartet distance between the topologies using DARwin 5 (Perrier and Jacquemoud-Collet 2006).

Because all phylogenetic approaches were highly congruent (Results), the topology resulting from the Bayesian chronogram was used for the following analyses (see below). Because missing data can have an influence on the phylogenetic reconstruction (Wiens 2005) searches using the ML and non-ultrametric Bayesian approaches were also performed on a reduced dataset containing only those taxa harbouring at least half of the sequence-length (Supplementary material Appendix 2, Table A1, Fig. A5, A6), yielding results similar to those obtained when using the complete dataset (Supplementary material).

Phylogenetic α diversity

We measured the phylogenetic α diversity with the modified version of the *Rao* quadratic entropy index recently proposed in de Bello et al. (2010) including the correction of Jost (2007). Because this analysis relies on niche conservatism, we measured the phylogenetic signal in average degree-days in the butterfly of the study area using Blomberg's K (Blomberg et al. 2003). Higher K-values indicate that close relatives are more similar in their niche. A critical aspect of testing for trait convergence and divergence is the use of an appropriate null model that focuses only on the ecological mechanisms under study (Harvey et al. 1983). Detecting deterministic processes requires that possible differences in community structure resulting from phylogenetic relatedness be identified with an appropriate test. We built null models by reshuffling the tip label on the phylogeny in a way that preserved the frequency of important properties over the study area (e.g. species prevalence, species richness, Mouillot et al. 2007). Tip randomisation was selected over other approaches because it is equivalent to testing the null hypothesis that phylogeny is not an important component in structuring butterfly communities (see Pottier et al. in press for a similar approach with functional traits).We compared the observed diversities to those obtained from 9999 null models.

To identify the nature of an eventual community structuring process, we computed a standardized effect size (SES) for the *Rao* values calculated as proposed in Webb et al. (2002), as follows:

$$\text{SES-}Rao = \frac{(Rao_{obs} - \overline{Rao}_{sim})}{\sigma Rao_{sim}}$$

where Rao_{obs} is the observed *Rao* value, $\overline{Rao}_{sim}$ is the average of the *Rao* values simulated under the null model, and σRao_{sim} is their variance. Here, positive SES-*Rao* values indicate phylogenetic divergence, while negative values indicate phylogenetic similarity. This standardisation of the *Rao* index allows for a better comparison of phylogenetic diversity across different butterfly communities (Webb et al. 2002) and allows inferring the magnitude of difference between the observed structure and the expected result under stochastic processes. We used a permutation test to evaluate if the relationship between the environmental factors and the phylogenetic α diversity holds when the factor is randomized.

To determine the contribution of each butterfly family to the phylogenetic community structure at each location, we calculated the proportion of butterflies belonging to each family at sites with 1) negative SES-*Rao* values (below the 25th percentile, indicating clustering) and degree-day values below 1500; 2) negative SES-*Rao* values (below the 25th percentile, indicating clustering) and degree-day values above 1500; and 3) positive SES-*Rao* values (above the 75th percentile, indicating overdispersion). A limit of 1500 degree-days was chosen because it represents the forest limit that separates the mountain and subalpine belts in this region of the Alps (Pellissier et al. 2010). Beyond this limit, the environment becomes rapidly more stressful, which impacts the structure of communities (Pellissier et al. 2010). The 25th and 75th percentiles were chosen to obtain an overview of the family composition in communities with relatively higher and lower phylogenetic α diversities.

Phylogenetic β diversity

We measured the phylogenetic β diversity with the same modified version of the *Rao* quadratic entropy index as α diversity (see above). β diversity measures variation among communities (Whittaker 1975) and is defined as the pairwise difference between the total diversity γ between two sites and the mean local α diversity. We used the randomization procedure as used for the calculation of phylogenetic α diversity, reshuffling the tip label on the phylogeny to obtain 9999 null models. Kraft et al. (2011) raises general doubts about analyses of β diversity, suggesting that variation may

be a simple artefact of differences in the species pool. In order to deal with this issue, we used null models described above to identify pairs of communities for which the phylogenetic β diversity was much higher (95th percentile) and lower (5th percentile) than expected under the 9999 null models, which corresponded to smaller or larger turnover rates of phylogenetic community structure. Afterwards, we used Mantel tests to assess if significantly dissimilar community pairs were more different in terms of degree-days and plant species richness to non-significantly dissimilar community pairs.

Results

Overall diversity

We found 122 butterfly species (14 Hesperiidae, 15 Pieridae, 4 Papilionidae, 1 Riodinidae, 59 Nymphalidae, 29 Lycaenidae) in the studied area (Supplementary material Appendix, Table A2), representing more than half of the species currently known to occur in Switzerland, and did not include any thermophilous species known for the country. Butterfly species richness was highly variable across the sampled sites. We found up to 52 butterfly species in plant-rich grasslands situated in warmer areas at low elevation, whereas no species were found at some high-elevation sites. Because occurrences of the butterfly species from our dataset had a low spatial autocorrelation (mean Moran's $I = 0.14$, range $= -0.04$ to 0.55), we can be confident about the spatial independence of the inventoried sites.

Our results show that the butterfly species richness was positively correlated to degree-days ($p < 0.0001$, Fig. 2a). In turn, the residuals of this relationship were positively correlated to plant species richness ($p < 0.0001$, Fig. 2b). Note that we also tested quadratic terms, but only linear terms were significant.

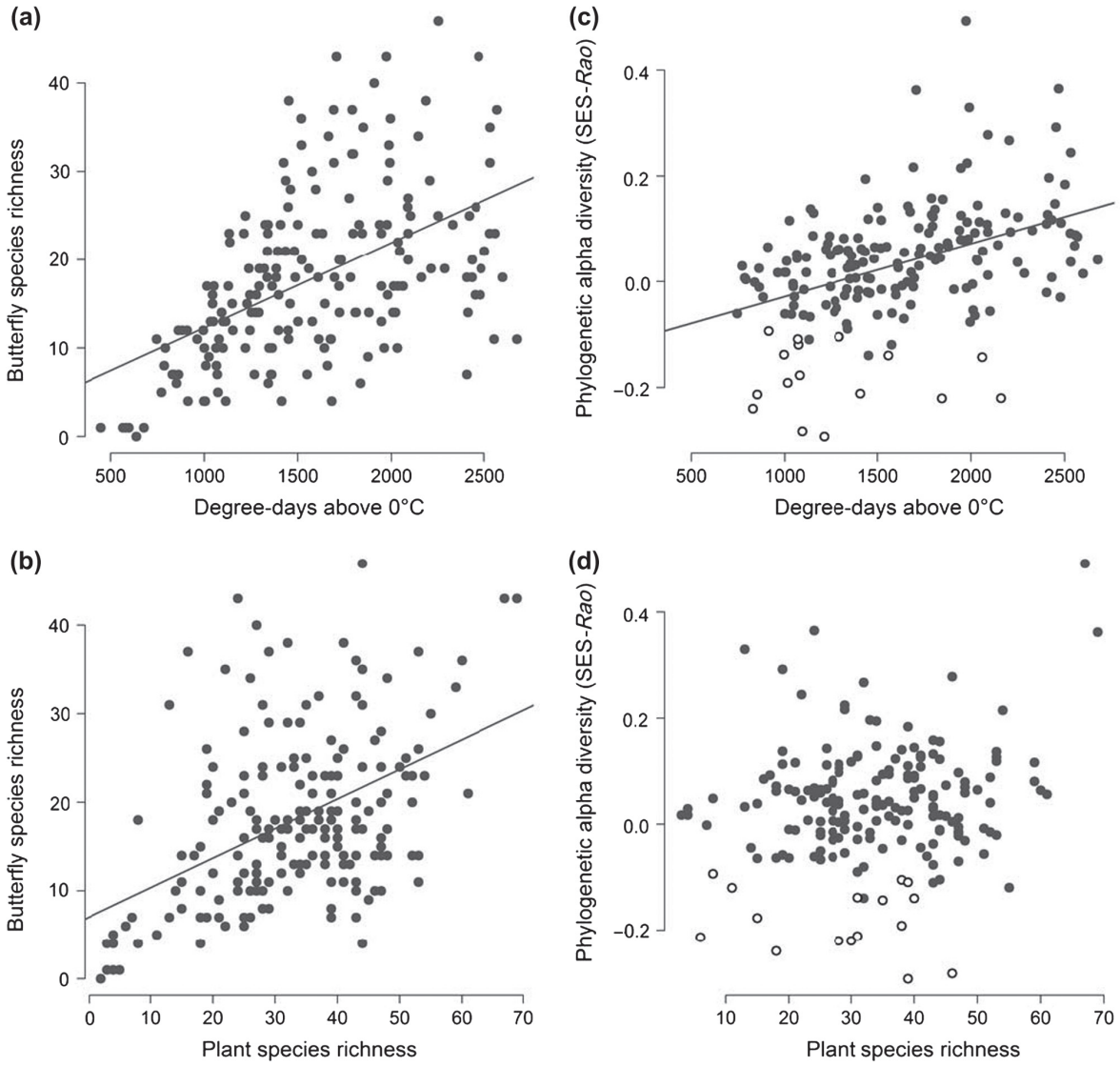

Figure 2. Correlation between degree-days (a, c) and plant species richness (b, d), and butterfly species richness (a, b) and SES-*Rao* of butterfly phylogenetic diversity (c, d). Negative SES-*Rao* values indicate α diversities lower than those computed with null-models, while positive SES-*Rao* values indicate α diversities higher than those computed with null models. Circles represent sampled locations. Empty circles represent significantly clustered communities.

Phylogenetic inferences

The tree topologies inferred from the ML and Bayesian estimations provided highly congruent results. The mean quartet distance between the three topologies was close to 1%, meaning that 99% of the tree components were identical (Supplementary material). The primary differences concerned some terminal nodes that were not well supported in some of the methods (Supplementary material Appendix 2, Fig. A2, A3, A4). Deep nodes were particularly well supported in all approaches and presented only one single node-incongruence between the ultrametric and non-ultrametric Bayesian approaches (Supplementary material Appendix 2, Fig. A4). All families were particularly well-supported in the Bayesian reconstructions. The two most basal clades were those corresponding to the Papilionidae and Pieridae families. Our results not only retrieved the monophyly of the families, but also that of the subfamilies. Our results are fully congruent with those obtained by Heikkilä et al. (2012). For convenience and because the phylogenetic signal was higher (see below, Litsios and Salamin in press), we will hereafter only refer to the results obtained through ultrametric Bayesian approaches.

Phylogenetic α diversity

We found a significant phylogenetic signal in the temperature niche with the chronogram ($K = 0.42$, $p = 0.01$) but not with the phylogram ($K = 0.14$, $p = 0.12$). Variance in phylogenetic α diversity (SES-*Rao*) was positively correlated to degree-days (DDEG: $p < 0.0001$, Fig. 2c). The residuals of this relationship were not correlated to plant species richness (PLRI: $p = 0.35$, Fig. 2d). The increase of phylogenetic diversity along the gradient of degree-days suggests stronger environmental filtering toward higher elevation (Fig. 2c). The communities with the lowest phylogenetic diversities were significantly less diverse than expected from the null models (Supplementary material Appendix 3, Fig. A7, example of distribution of simulated values). Out of the 192 analysed communities, 16 (8%) were significantly different ($p < 0.05$) from the null expectation based on phylogenetic tree tip randomisation (open circles in Fig. 2c, d). The most phylogenetically clustered communities occurred in cool environments at high elevations (Fig. 2c, d) above the treeline (< 1500 degree-days). Yet, a few were also found at higher-temperature sites and were exceptions to this trend. No communities had higher phylogenetic α diversities than expected from the null models derived by phylogenetic tree tip randomisation. We found highly similar results when using the net relatedness index (NRI) as implemented in the picante package (Kembel et al. 2010, Supplementary material Appendix 3, Fig. A8). The analysis of the composition within clustered communities indicated that the clustering was caused by the poor representation of members of the families Lycaenidae and Hesperiidae in those communities with an overrepresentation of Nymphalidae (Fig. 3).

Phylogenetic β diversity

When considering the Bayesian chronogram, 1714 pairs of communities were significantly more dissimilar in phylogenetic β diversity than expected from the null-models, while 458 pairs were significantly more similar. In particular, Mantel tests indicated that the significantly more dissimilar pairs of communities were more dissimilar in terms of degree-days values and not in terms of plant species richness (DDEG: $r = 0.19$, $p = 0.0001$, PLRI: $r = 0.08$, $p = 0.34$, Fig. 4a, b). We found no significant effect

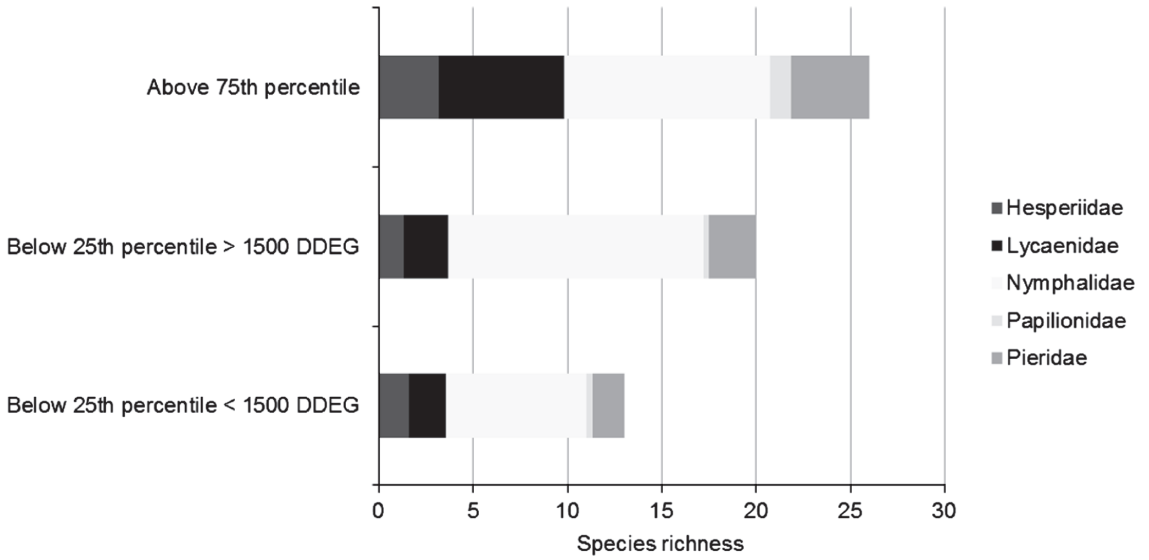

Figure 3. Proportional representation of butterflies in the five Papilionoidea families (Hesperiidae, Lycaenidae, Nymphalidae, Papilionidae and Pieridae) found in 1) communities occurring below 1500 degree-days (DDEG) with α phylogenetic diversity below the 25th percentile, 2) communities occurring above 1500 degree-days with α phylogenetic diversity below the 25th percentile and 3) communities with α phylogenetic diversity above the 75th percentile. The bar length represents the average species richness in communities. *Hamearis lucina*, the unique Riodinidae comprised in this study, was omitted.

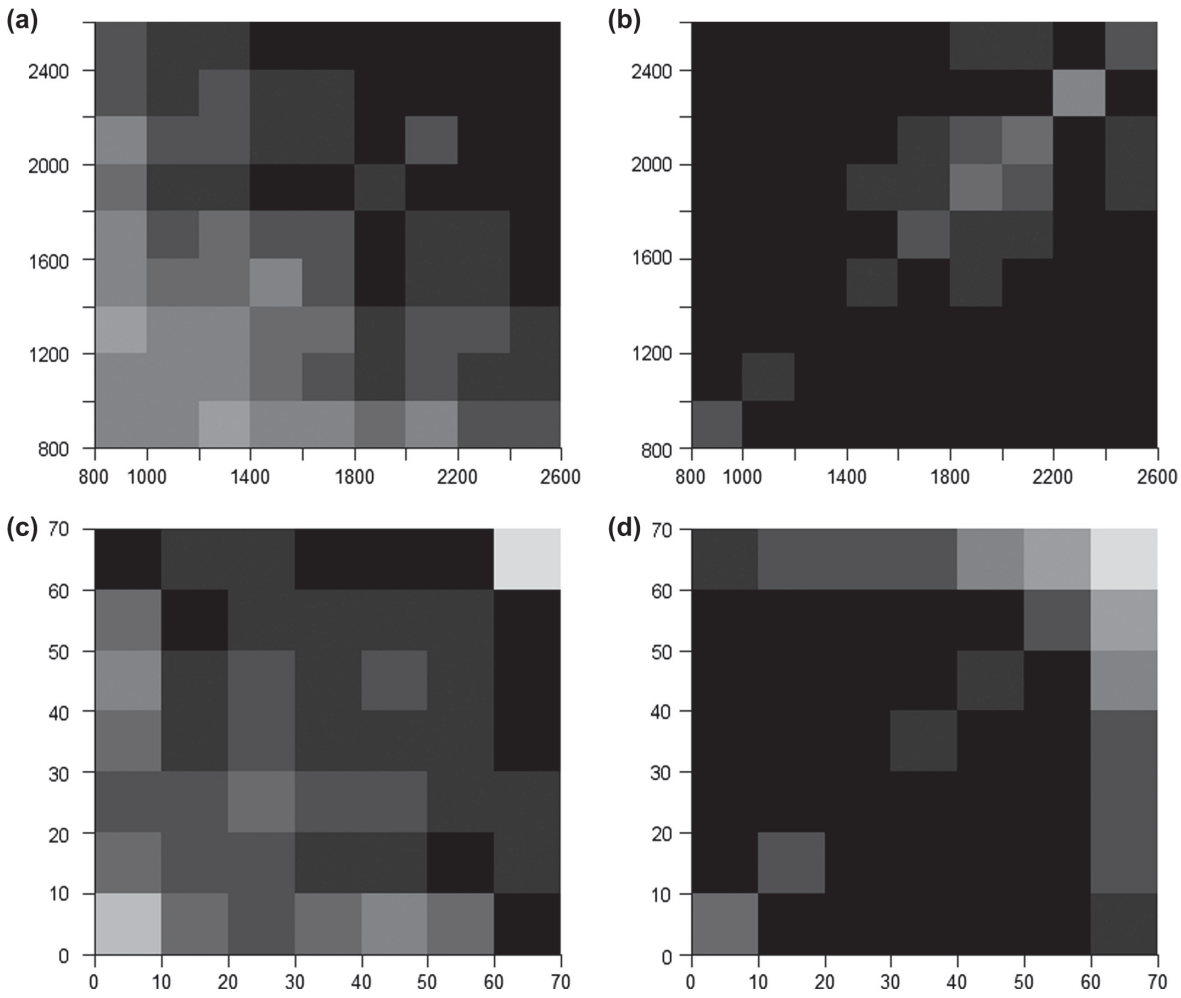

Figure 4. Classes of degree-days (a, b) and plant species richness (c, d) encompassing more different or similar pairs of communities as regards to their phylogenetic β diversity. (a) Values for pairs of communities more significantly dissimilar than expected by the null models as regards to degree-days. (b) Values for pairs of communities more significantly similar than expected by the null models as regards to degree-days. (c) Values for pairs of communities more significantly dissimilar than expected by the null models as regards to plant species richness. (d) Values for pairs of communities more significantly similar than expected by the null models as regards to plant species richness. Colour intensity of pixels is proportional to the number of compared pairs of communities presenting that given value combination (light: high; dark: low).

of geographic distances alone on significant dissimilarities among communities ($r = 0.05$, $p = 0.5$). Results were similar when considering the Bayesian phylogram (Supplementary material Appendix 3, Fig. A9).

Discussion

Growing evidence of non-random trait or phylogenetic dispersion in communities supports niche based assembly (Weiher et al. 2011). In particular, variation in environmental conditions can cause variation in phylogenetic structures both within and among communities (Graham et al. 2009). Our phylogenetic α diversity results indicate that cold temperatures at high elevations likely prevent the successful colonization of non-adapted species generating communities mostly composed of closely related species (Fig. 2c). In addition, while butterfly species richness in communities is significantly related to plant species richness (Fig. 2b) we found no general effect of plant species richness on phylogenetic α and β diversities (Fig. 2d).

The climatic conditions at high elevation (i.e. low temperatures; Körner 2007) prevent the colonization of non-adapted lineages as suggested by our results on the phylogenetic clustering of communities (open circles in Fig. 2c, e). Because butterflies are of tropical origin and tend to show climatic niche conservatism (Hawkins 2010), only a restricted number of taxa have adapted to colder environments and are able to survive at high elevations. The environment thus filters closely related species that share traits conferring the ability to tolerate severe climates. Karl et al. (2009) provided strong support for the idea that selection for a particular allele (PGI enzyme) in high elevation populations of *Lycaena tityrus* conferred resistance to cold temperatures. In our case, similar adaptations in the family Nymphalidae – and more specifically in the *Erebia* and *Boloria* genera − could also explain the relative dominance of this family at high elevations (Pellissier et al.

2012a, b). In contrast, members of the family Lycaenidae are rare at higher elevations (Fig. 3). Lycaenids participate in a wider range of ecological interactions than perhaps any other Lepidoptera, as they display mutualistic interactions with ants (Fiedler 1991, New 1992). A change in the cost-benefit ratio of mutualism along the elevation gradient or the absence of their specific food plant may explain their absence from high elevations (Pellissier et al. 2012a). Our results also indicated higher β diversities among communities at colder temperatures (Fig. 4a). The environment is more heterogeneous with patches of vegetation interspersed with bare rock and scree (Körner 2003), which, in turn, may increase the variability of the butterfly communities within high elevation areas (Gutiérrez and Menéndez 1998). Species dispersal abilities may facilitate successive colonization of suboptimal habitats at high elevation, paralleling the mass effect documented in plants (Gryntes et al. 2008).

High values of plant species richness and warmer climatic environments allow for richer and more phylogenetically diverse butterfly communities (Fig. 2c, d). We found that the phylogenetically most diverse butterfly communities occur under warmer conditions (Fig. 2c, e). However, these communities were never more diverse in term of phylogenetic diversity than expected based on null models, suggesting that limiting similarity between butterfly species is not detectable in these communities. It appears that more benign climatic conditions allow more butterfly species to inhabit lower elevation habitats, phylogenetically diverse, but never more than expected from null-models.

Given the phylogenetically structured host–plant preferences in butterfly (Ehrlich and Raven 1964), we would have expected a significant correlation between plant species richness and SES-*Rao*. Yet, the SES-*Rao* of the phylogenetic α diversity was not significantly related to plant species richness. This could suggest that a decrease in plant species richness as potential reduction in biotic resources primarily affects the butterfly species richness. Yet, this may also be because the plant species richness is a too coarse descriptor of trophic resource range for butterflies and finer indicators (e.g. plant phylogenetic diversity) should be investigated and considered in future studies. Several butterfly communities from warm conditions had lower phylogenetic α diversities when compared to null models (open circles in Fig. 2e). The clustering observed in our study at lower temperatures, reflected a decrease in the representation of the Lycaenidae and Hesperiidae families (Fig. 3), families that are known as habitat specialists or poor dispersers (New 1992). Species displaying those characteristics are strongly and negatively affected by intensive land use (Ekroos et al. 2010). Indeed, many species of lycaenid larvae are myrmecophilous and lycaenids and hesperiids have restricted host-plant ranges (Stadler et al. 2003). In our study area, land use intensification can have a considerable negative impact on plant species richness in some grasslands, which may affect the available plant resources for butterflies and in turn decrease the phylogenetic diversity of communities.

One caveat of our approach is that the inferences are limited by the correlative framework. Many other environmental factors may co-vary with elevation in addition to degree-days including precipitation and winds (Körner 2007). Also, alpine environments at high elevations often form a series of patchy habitats with strong fluctuations in physical factors, such as greater daily and seasonal climatic variability (Brinck 1974), and a more unstable substrate due to the predominance of exposed rock surfaces and shallow soils subject to erosion and solifluction (Körner 2003). Second, historical processes may also generate non-random phylogenetic structure in communities (Leibold et al. 2010, Thiel-Egenter et al. 2011). However, the study area is small with no major biogeographic boundaries. The observed pattern is thus more likely to arise from ecological rather than historical processes.

Our study suggests that temperature may directly affect the phylogenetic diversity of butterflies. Hence future climate change may cause phylogenetically non-random extinctions in communities (Thuiller et al. 2011). In colder and more severe conditions deterministic filtering processes prevail over purely stochastic events in assembling the communities of butterfly adapted to severe conditions. This specialized fauna at high elevation, principally composed of species of the family Nymphalidae, is likely to be the first to suffer losses in response to climate change. Moreover, more intensive land use is also expected to have a negative effect on natural habitats and species diversity (Foley et al. 2005, Forister et al. 2010). The loss of species with respect to land use variation may also not be phylogenetically random and will likely lead to a loss of phylogenetic diversity. Sensitive clades such as the family Lycaenidae are likely to disappear more quickly, leading to homogenised communities.

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Supplementary material (Appendix E7716 at <www.oikosoffice.lu.se/appendix>. Appendix 1–3.