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Mutualistic Mimicry and Filtering by Altitude Shape the Structure of Andean Butterfly Communities

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ABSTRACT: Both the abiotic environment and abiotic interactions among species contribute to shaping species assemblages. While the roles of habitat filtering and competitive interactions are clearly established, less is known about how positive interactions, whereby species benefit from the presence of one another, affect community structure. Here we assess the importance of positive interactions by studying Andean communities of butterflies that interact mutualistically via Müllerian mimicry. We show that communities at similar altitudes have a similar phylogenetic composition, confirming that filtering by altitude is an important process. We also provide evidence that species that interact mutualistically (i.e., species that share the same mimicry wing pattern) coexist at large scales more often than expected by chance. Furthermore, we detect an association between mimicry structure and altitude that is stronger than expected even when phylogeny is corrected for, indicating adaptive convergence for wing pattern and/or altitudinal range driven by mutualistic interactions. Positive interactions extend far beyond Müllerian mimicry, with many examples in plants and animals, and their role in the evolution and assembly of communities may be more pervasive than is currently appreciated. Our findings have strong implications for the evolution and resilience of community structure in a changing world.

Keywords: community ecology, altitudinal gradient, Müllerian mimicry, phylogenetic structure, Ithomiini, Andes.

Introduction

Assemblages of coexisting species result from past and present ecological and evolutionary processes. Local climate, usually estimated by measures of energy or productivity, and habitat heterogeneity, such as topography, appear to be correlated with community diversity (Hawkins et al. 2003). At the same time, interactions among

species, such as predation, competition, and mutualism, play a determinant role in species distribution and therefore in community composition. Altitudinal gradients offer excellent opportunities to study the effect of environmental heterogeneity on species assemblages as they correlate with many environmental variables, especially temperature and moisture (Hodkinson 2005). In addition, vegetation assemblages vary across altitudinal gradients and contribute to environmental heterogeneity (Homeier et al. 2010). Furthermore, global biodiversity peaks in tropical montane regions (e.g., Orme et al. 2005; Grenyer et al. 2006), and a number of authors have suggested that montane regions are important drivers of diversification (Thomas et al. 2008; Elias et al. 2009*b*; Rosser et al. 2012). The limited areas of many montane habitats mean that montane species tend to have much smaller geographic ranges than lowland continental species, and it is therefore unsurprising that threatened species are also concentrated in montane regions (Orme et al. 2005; Grenyer et al. 2006). Understanding the ecological and historical processes and factors that shape communities in montane regions is consequently of interest for both understanding and conserving global biodiversity.

In the past decade, there has been increasing effort to use phylogenetic approaches to better understand community ecology by inferring processes that shape community structure from the phylogenetic structure of the community (Webb et al. 2002). Communities are primarily shaped by neutral processes, such as drift and random dispersal (Hubbell 2001), and nonneutral processes, which are ultimately governed by species traits. Nonneutral processes include adaptation to particular conditions or habitats; antagonistic interactions between species, such as competition, parasitism, and predation, which can limit species coexistence; and positive interactions, such as mutualism or facilitation, which promote species coexistence.

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Webb et al. (2002) proposed a framework for exploring the processes structuring communities by using the phylogenetic relatedness of species as a proxy for their ecological similarity. Their work focused mostly on two processes: (1) habitat filtering, whereby only species with specific adaptations can occur in a given habitat, eventually leading to communities that consist of ecologically similar species; and (2) competition, which limits coexistence of ecologically similar species, eventually leading to communities that consist of ecologically dissimilar species. Webb et al. (2002) posited that if underlying traits are phylogenetically conserved (i.e., more similar among related species), then habitat filtering should result in closely related species co-occurring more often than expected under random species distribution (phylogenetic clustering), whereas competition should result in closely related species co-occurring less often than expected under random species distribution (phylogenetic overdispersion). However, underlying traits might not be phylogenetically conserved if adaptive trait evolution is an important cause of speciation, and similarity in traits across species might instead represent convergent evolution. For instance, convergence in a trait underlying adaptation to a particular habitat occurs when multiple lineages adaptively diversify across habitats or niches (adaptive radiation). If traits are convergent, then habitat filtering is expected to result instead in phylogenetic overdispersion, while competition is expected to lead to a random species distribution with respect to phylogeny (Webb et al. 2002). Community phylogenetics can therefore potentially shed light on the importance and the modalities of habitat filtering and other ecological interactions in shaping community structure in montane regions.

Although most efforts in phylogenetic community ecology have focused on habitat filtering and competition, an increasing number of studies have emphasized the role of positive interactions among potential competitors in communities. Particularly widespread positive interactions include, for instance, facilitation in plants or other organisms via nursing (Valiente-Banuet and Verdu 2007; Brooker et al. 2008; Verdu et al. 2009) or shared pollinators or seed dispersers (e.g., Moeller 2004); formation of multispecies groups or flocks (Bshary and Noe 1997); and Müllerian mimicry (Müller 1879; Rowland et al. 2007). Positive interactions reduce abiotic or biotic stress, thereby fostering coexistence even between potential competitors (Gross 2008). Positive interactions might therefore have a strong impact on community composition, stability, and resilience, particularly in stressful environments (Kefi et al. 2008). Interactions between species suffer a high risk of being lost in montane habitats, because changes in abiotic and biotic conditions take place over short spatial distances along altitudinal gradients, increasing community disas-

sembly (Sheldon et al. 2011). The effect of climatic changes might be particularly dramatic in montane communities of species that interact positively, adding to the vulnerability of these already often range-restricted species. Yet among the few phylogenetic studies that have addressed the impact of positive interactions in community structure (Valiente-Banuet and Verdu 2007; Verdu et al. 2009; Alexandrou et al. 2011), none have examined their importance in montane ecosystems.

Here we investigate jointly the importance of habitat filtering by altitude and positive interactions in communities of Müllerian mimetic butterflies in the eastern Andes, the most diverse ecosystem on Earth (Myers et al. 2000). Müllerian mimicry in butterflies (Müller 1879) is a compelling example of positive, mutualistic interactions (Rowland et al. 2007), where different species protected by chemical defenses converge in warning color patterns (comimetic species; fig. 1C) and share the density-dependent cost of educating predators (primarily insectivorous birds; Mallet and Barton 1989; Kapan 2001). One of the most outstanding examples of Müllerian mimicry is the species-rich butterfly tribe Ithomiini (Nymphalidae: Danaeinae, ~380 species), which numerically dominate Neotropical forest understory butterfly communities and are mimetic models for a number of other Lepidoptera (Beccaloni 1997a). Ithomiine butterflies occur in humid forest habitats throughout the Neotropics, from sea level to about 3,000 m, and locally form multiple mimicry complexes (e.g., Beccaloni 1997a). Previous studies of ithomiine butterflies have found mimicry to play an important role in shaping within-community structure, in terms of species distribution across microhabitats and host plants (Beccaloni 1997b; DeVries et al. 1999; Willmott and Mallet 2004; Elias et al. 2008; Hill 2010). Moreover, phylogenetic evidence supports an adaptive association between microhabitat and mimicry (Elias et al. 2008), whereby comimetic ithomiine species share microhabitats more often than predicted by the phylogeny. This suggests adaptive convergence in microhabitat use among comimetic species driven by predator heterogeneity across microhabitats (Gompert et al. 2011). At a much larger scale, heterogeneous distribution of insectivorous birds across environmental gradients, especially altitudinal bands in tropical montane regions (Patterson et al. 1998), could potentially lead to adaptive association between habitat and mimicry structures. Yet shifts in altitudinal range, which correlate with numerous abiotic and biotic variables, may be much more phylogenetically constrained than shifts in microhabitats. A number of recent studies have indeed suggested that shifts in altitudinal range in Andean butterflies are relatively uncommon and often followed by diversification of a clade within a particular altitudinal band (e.g., Willmott et al. 2001; Elias et al. 2009b, 2009c; Casner and Pycrz

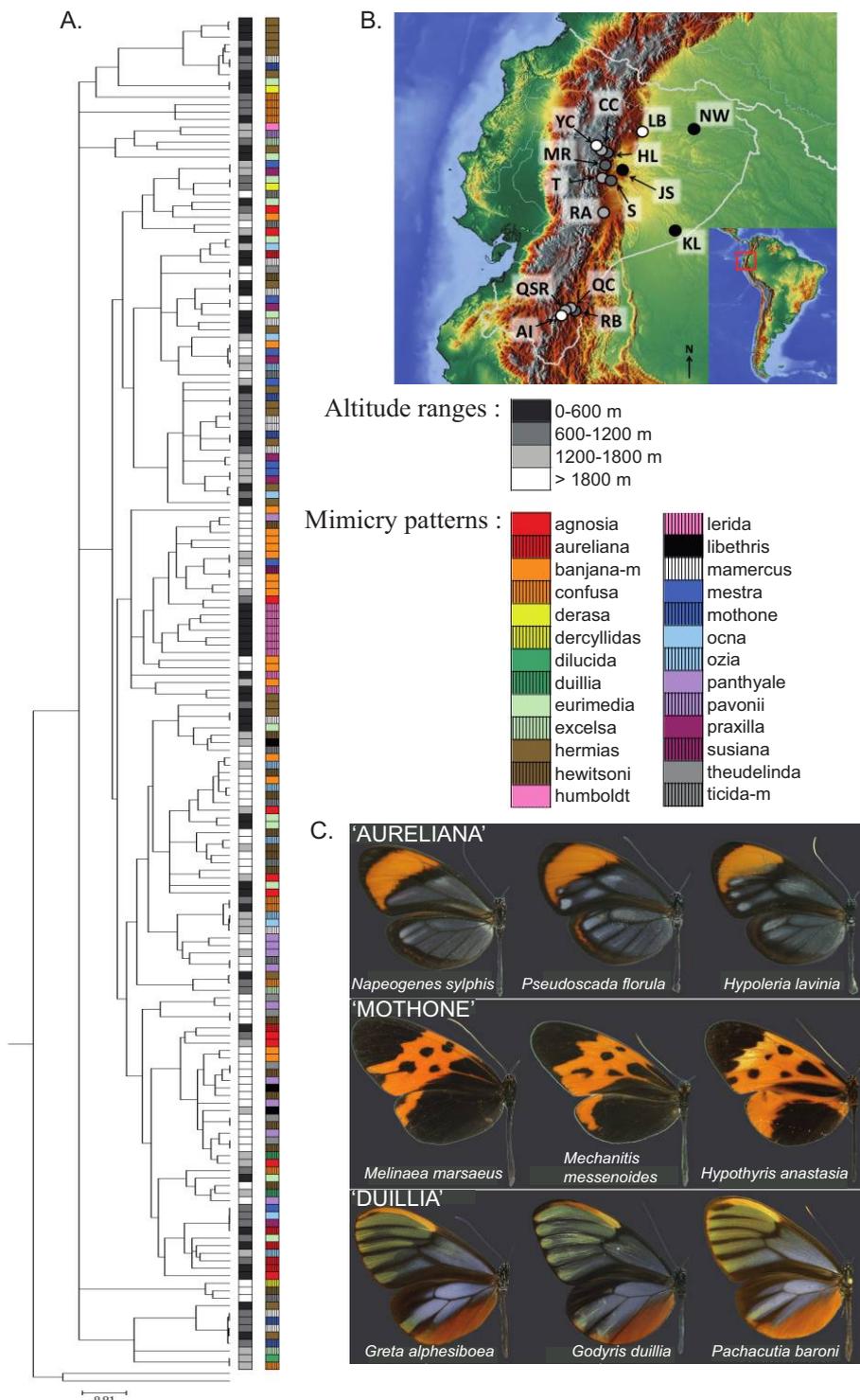


Figure 1: A, Phylogenetic tree for 180 ithomiine taxa (154 species) and two out-groups. All nodes having a posterior probability below 80% were collapsed. In this figure, each species was assigned to an altitude interval based on mean altitude per species, indicated in the first column. Mimicry patterns are indicated in the second column. B, The 15 sites are mapped with the same altitude color code as in the phylogeny. Full names of sites are given in table 1. C, Examples of three mimicry patterns shared by distantly related Ithomiini species. Each mimicry pattern is indicated in the upper left corner of each row.

2010). However, cases of parapatric speciation along the slopes of the Andes have also been reported (Hall 2005), suggesting adaptive radiation across altitudinal bands. The outcome and implications of filtering by altitude and mutualistic interactions in montane communities of mimetic butterflies are therefore difficult to predict.

In this article, we use incidence, abundance, and phylogenetic data from up to 15 sites in the eastern Ecuadorian Andes to address several questions. First, are communities primarily structured by filtering by altitude, and does this reveal phylogenetic constraints (indicated by phylogenetic clustering) or adaptive radiation (indicated by phylogenetic overdispersion)? To address this question, we examine the phylogenetic structure of communities and how it relates to altitude. Second, do species that interact mutualistically co-occur more often than expected at random? With this in mind, we investigate patterns of co-occurrence of comimetic species and how mimicry relates to altitude, independently of the phylogeny. Finally, are mutualistic interactions powerful enough to drive an association between mimicry and altitude that is stronger than that predicted by the phylogeny? To answer this question, we examine whether mutualistic species occur at similar altitudes more often than predicted by the phylogeny.

Material and Methods

Data

Two data sets were analyzed, representing two components of ithomiine community structure. The first data set (in-

cidence data set) was generated by collating incidence (i.e., presence/absence) data obtained from our own field inventories supplemented by specimen data from multiple museum and private collections, for a total of 15 sites in eastern Ecuador (table 1; fig. 1B). This data set, which ignores abundances since abundance data were not collected at all sites, aims at representing most of the diversity present in these sites. We obtained data for 155 species at these 15 sites, representing 90% of the total of 173 species that are estimated to be potentially present across all of these sample sites on the basis of known broad altitudinal and geographic distributions (K. R. Willmott and J. P. W. Hall, unpublished data).

The second data set (abundance data set) was generated by sampling over short periods of time (2 months per site) seven of the above-mentioned sites to obtain abundance data for ithomiine species (table 1). Estimating species abundances over a short time frame gives us the opportunity to study individuals that effectively coexist and consequently interact. We sampled by walking trails within a restricted area (1–3 km²), using 1- to 8-m-long hand nets and attempting to capture all individuals encountered (Elias et al. 2008). Individuals were identified to species in the field. Where necessary, vouchers were kept for molecular analyses, and remaining individuals were marked and released where they were captured. Abundance data for an additional site (also represented in the incidence data set) was obtained from the literature (Beccaloni 1997b; table 1). We sampled at sites within at least two biogeographic regions (based on subspecies distributions)

Table 1: Sites sampled, code names, altitude, geographic coordinates, species richness, and mimicry richness (number of identified mimicry complexes)

Site	Code	Altitude (m)	Location	Species richness		Mimicry richness		No. individuals
				Ab	In	Ab	In	Ab
Napo Wildlife Center (Añangu)	NW	200	.52°S, 76.4°W	56	56	8	8	1,232
Jatun Sacha	JS	450	1.07°S, 77.6°W	41	57	9	9	1,361
Mariposa	MR	650	.91°S, 77.79°W	33	33	8	8	412
Hollín	HL	1,100	.69°S, 77.73°W	19	19	12	12	86
Quebrada Los Chorrillos	QC	1,250	4.03°S, 79°W	26	33	17	17	574
Cocodrilo	CC	1,600	.65°S, 77.79°W	39	39	18	18	326
Arcoiris	AI	2,000	3.99°S, 79.09°W	53	53	12	12	2,166
Yanayacu (Cosanga)	YC	2,100	.6°S, 77.88°W	32	32	7	7	721
Kapawi Lodge	KL	250	2.56°S, 78.85°W		48		8	
Río Bombuscaro	RB	1,000	4.11°S, 78.96°W		17		10	
Shell	S	1,050	1.49°S, 78.06°W		22		12	
Topo	T	1,300	1.4°S, 78.2°W		24		12	
Río Abanico	RA	1,550	2.25°S, 78.2°W		39		14	
Quebrada San Ramón	QSR	1,700	3.97°S, 79.08°W		21		13	
La Bonita	LB	2,200	.56°S, 77.52°W		40		11	

Note: Ab = abundance data set (2 months' field collections), In = incidence data set (collated from all data available for these communities). The last column shows the total number of individuals collected at each site in the abundance data set.

for the main altitudinal bands (lowlands: below 900 m; midaltitude: 900–1,500 m; high altitude: above 1,500 m). This data set is composed of 6,878 individuals and 146 species (table 1; incidence and abundance data sets are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.1534j> [Chazot et al. 2013]).

In both data sets, each site has an altitudinal range smaller than 50 m, while the total range spanned across sites ranges from 200 m to 2,200 m. Each ithomiine species was assigned to a mimicry complex based on consideration of pattern similarity (fig. 1C) and congruence in geographic phenotypic variation, following classifications used in previous studies (Beccaloni 1997a; Jiggins et al. 2006). For all analyses requiring the altitudinal distribution of species, we used a database of 3,193 species-locality records (an average of ~20 localities per species) compiled by K. R. Willmott from 20 years of field and museum research, representing all taxa included in our study. We ran the analyses separately with minimum, maximum, median, and mean altitudes. Since different measures of altitude returned similar results, here we present only those obtained with mean altitude.

Phylogeny

We generated a Bayesian molecular phylogeny of all species except *Episcada polita*, for which we did not have tissue. *Episcada polita* was consequently removed from the incidence data set (*E. polita* was not found in the abundance data set). We used one nuclear gene fragment (EFl α : 1,258 bp) and a mitochondrial fragment that spanned three genes (COI-tRNA^{Leu}-COII: 2,366 bp). Twenty-four species exhibited two subspecies or forms that differed in mimicry pattern, and one species exhibited three subspecies. In order to perform mimicry-related analyses while accounting for the fact that different subspecies belong to the same species, we considered these subspecies or forms as distinct taxa in the phylogeny but with identical sequences, such that subspecies or forms of the same species had phylogenetic distances of 0. We also added two out-groups (*Lycorea halia* [Danaini] and *Tellervo zoilus* [Tellervini]) to root the tree (fig. 1A). The phylogeny, therefore, consisted of 180 ithomiine taxa (154 species) and two out-groups. For 71 species, sequences were downloaded from GenBank (<http://www.ncbi.nlm.nih.gov/genbank/>). Sequences of six species were kindly provided by colleagues, and we sequenced the remaining 79 species (GenBank accession numbers are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.1534j> [Chazot et al. 2013]; polymerase chain reaction conditions followed Elias et al. 2009b).

We first generated separate phylogenies for the mitochondrial and nuclear regions using Bayesian Inference (see apps. A and B; apps. A–D available online; trees and

data sets are deposited in TreeBASE: <http://purl.org/phylo/treebase/phylo/study/TB2:S14604>). We then combined both genes and ran PartitionFinder, version 1.0.1. (Lanfear et al. 2012), to choose partitions, allowing all possible partitions. Following PartitionFinder results, we partitioned our data set into two: one partition encompassing COI (codon positions 1+2)-tRNA^{Leu}-COII (codon positions 1+2)-EFl α and one partition encompassing COI (codon position 3)-COII (codon position 3). Both partitions followed a GTR+I+ Γ model. We performed two runs of 30,000,000 states, each using BEAST 1.7.1 (Drummond et al. 2012). The trees were generated under a Yule process with an uncorrelated lognormal relaxed clock to obtain relative time divergences between species. We used the AWTY program (http://king2.scs.fsu.edu/CEBProjects/awty/awty_start.php) to check that the runs had converged to the same optimum. We combined the two runs with a 25% burn-in and extracted the maximum clade credibility tree using the median of branch lengths of all remaining trees (TreeAnnotator; Drummond and Rambaut 2007). The resulting tree is well resolved (83% of nodes having a posterior probability higher than 0.95) and is consistent with published molecular and morphological phylogenies of Ithomiini (Brower et al. 2006; Jiggins et al. 2006; Willmott and Freitas 2006; Elias et al. 2008, 2009b; de-Silva et al. 2010; see app. C). To take into account phylogenetic uncertainty, we collapsed all nodes having a posterior probability lower than 80%. This collapsed tree was used in the analysis.

Phylogenetic Structure of Communities

To examine phylogenetic structure among communities, we used Hardy and Senterre's indexes: I_{ST} , P_{ST} , and Π_{ST} (Hardy and Senterre 2007). These indexes are analogous to genetic population indexes F_{ST} and G_{ST} , and partition species and phylogenetic diversity within and among communities. More precisely, I_{ST} ignores phylogenetic information and uses only species identity and abundances, thus expressing species turnover (Hardy and Senterre 2007). Meanwhile, P_{ST} uses relative abundance data and phylogenetic distances among species and thus expresses phylogenetic turnover. If there is no phylogenetic structure between communities, then $I_{ST} = P_{ST}$. If $P_{ST} < I_{ST}$, then co-occurring species are phylogenetically more distant than species at the regional scale (phylogenetic overdispersion, suggesting competition or adaptive radiation). If $P_{ST} > I_{ST}$, then co-occurring species are phylogenetically more related than species at the regional scale, showing phylogenetic clustering (habitat filtering). To test whether P_{ST} is significantly higher than I_{ST} (one-tailed test), we performed permutations of species on the tips of the whole phylogeny (Hardy and Senterre 2007). The last index,

Π_{ST} , also expresses species turnover, using species incidence and phylogenetic distances between species (i.e., abundances are ignored). The inequality $\Pi_{ST} < 0$ indicates phylogenetic overdispersion, whereas $\Pi_{ST} > 0$ indicates phylogenetic clustering. Similarly to P_{ST} , we permuted the species on the tips in the whole phylogeny to statistically test for $\Pi_{ST} > 0$ (one-tailed test; Hardy and Senterre 2007). We calculated global P_{ST} and Π_{ST} across all communities, which represent a mean signal of phylogenetic structure. We also estimated P_{ST} and Π_{ST} between pairs of communities. To investigate how phylogenetic structure relates to altitude, we used partial Mantel tests to test the relationship between these pairwise indexes and altitudinal distances between pairs of communities, controlling for geographic distance. We used log transformation of altitudinal distance to make the relationship with phylogenetic structure metrics linear. All indexes were computed with the software SPACoDI (Hardy 2010). The P_{ST} and Π_{ST} measures were used for the abundance data set, whereas only Π_{ST} was tested for the incidence data set.

We estimated phylogenetic diversity within communities using the mean phylogenetic distance between species (extracted from the phylogeny; Webb et al. 2008) and tested for a relationship with altitude using linear regression. As an illustration of the relationship between phylogenetic diversity and altitude, we investigated how the proportion of species belonging to the four most diverse genera in each community changes with altitude using linear regression. We finally tested independently the relationship between species richness, mimicry richness (number of identified mimicry complexes), and altitude using linear regression. All statistical tests were performed using R, version 3.0.1.

Mimicry Structure of Communities

Müllerian mimicry is expected to lead to the coexistence of species that share the same color pattern. As a consequence, comimetic species should coexist within communities more often than expected by chance, a pattern we hereafter refer to as “mimicry clustering.” We tested for mimicry clustering using Hardy and Senterre’s I_{ST} , using the abundance of mimicry complexes (instead of species) per community as follows. For the abundance data set, we summed the number of individuals (number of species in the incidence data set case) sharing the same mimicry pattern in each community to obtain abundance data per community for each mimicry complex and then calculated I_{ST} . In sexually dimorphic species (i.e., species where sexes belong to distinct mimicry complexes), males and females were counted separately. Next, observed I_{ST} was compared to null values obtained under the hypothesis of random community structure. To generate an appropriate

null distribution, we randomized mimicry patterns among species without changing species composition and abundances in each community (analogous to DeVries et al.’s [1999] and Hill’s [2010] test of mimicry structure across microhabitats), and for each randomization we estimated a new I_{ST} . If comimetic species are clustered within the communities, then observed I_{ST} should be higher than most values in the null distribution. We calculated the probability of obtaining by chance an observed I_{ST} value higher than that expected at random (one-tailed test).

To investigate how mimicry similarity relates to altitudinal distances, we calculated pairwise I_{ST} on mimicry abundances per community and performed partial Mantel tests between pairwise I_{ST} and pairwise altitudinal distances, controlling for geographical distances.

Phylogenetic Signal, Altitude, and Mimicry

Since we found mimicry clustering along the altitudinal gradient (association between mimicry and altitude; see “Results”), we further investigated the causes of this pattern. Specifically, an association between mimicry and altitude could be due to (1) common ancestry, if altitude and color pattern are both phylogenetically conserved, or (2) adaptive convergence, if mutualistic interactions have tightened comimetic species coexistence along the altitudinal gradient by causing convergence in altitude, color pattern, or both traits.

To test for phylogenetic signal in altitudinal niche (hereafter, “altitude”), we used a phylogenetic autocorrelogram that measures the similarity of altitude between pairs of species. Similarity is measured by an autocorrelation coefficient (Moran’s I ; Diniz and de Sant’Ana 2000). By dividing the phylogeny into different divergence time intervals, we can visualize how similarity varies with phylogenetic depth. We divided our phylogeny into six relative divergence time intervals with upper limits of 0.05, 0.1, 0.15, 0.2, 0.25, 0.30, and 0.35. The observed coefficient values were compared to two null models: (1) a model with no phylogenetic signal (mean autocorrelation coefficient close to zero), constructed by randomizing species on the tips of the phylogeny 1,000 times, and (2) a model of Brownian evolution, where trait evolves as a random walk with constant evolutionary rate through time. In the latter case, trait similarity is expected to be higher between species that have recently diverged and to decrease as divergence time increases. A Brownian null distribution was obtained by simulating the evolution of mean altitude 1,000 times.

To test for phylogenetic signal in color patterns, we performed a Mantel test between phylogenetic distances and mimicry distances for pairs of species. Mimicry distance between species was 0 if species had the same color

pattern and 1 if they did not share a pattern. We attributed intermediate values for sexually dimorphic species (10 species) as follows: mimicry distance was 0.5 between a monomorphic and a dimorphic species when one pattern was shared, 0.5 between two dimorphic species harboring the same patterns, and 0.75 between two dimorphic species that shared one pattern.

To test whether the association between mimicry and altitude was stronger than expected given the phylogeny (i.e., for convergence in color pattern among species at the same altitude and/or convergence in altitude among species with the same color pattern), we used two methods that were used by Elias et al. (2008). First, we performed a regression between mean altitudinal distances (obtained from the altitude database) and phylogenetic distances between pairs of species. If comimetic species tend to share altitude more often than expected given the phylogeny, then points corresponding to pairs of comimetic species should be mostly under the regression line. We computed the average value of residuals of pairs of comimetic species and compared it to a null distribution obtained by randomizing mimicry patterns among species 10,000 times. We calculated the probability of obtaining by chance the

observed value in the null distribution (one-tailed test). In the second method, we compared the observed association between mimicry and altitude, measured as the average distance in mean altitude between pairs of comimetic species standardized by the mean among all pairs of species, with the expected association under phylogenetic signal alone. A low value for this measure indicates a stronger association. To obtain a null distribution of our association measure, we simulated the evolution of mean altitude on the phylogeny under a Brownian model 10,000 times (this model of evolution was not rejected by our test of phylogenetic signal). The regression and simulation tests were run with both the abundance and incidence data sets.

Results

Phylogenetic Structure

There is a clear pattern of phylogenetic clustering within communities (table 2). Global Π_{ST} is significantly higher than 0 in both the abundance and incidence data sets, even after Bonferroni correction for multiple independent tests (table 2). Global P_{ST} is higher than I_{ST} in the abun-

Table 2: Statistical test results

	Obs	sim/ N	95% CI/ r_M	p
Abundance data set:				
Phylogenetic structure:				
Global P_{ST}	.0966	sim = .0817	(.0678; .1000)	.0487
Global Π_{ST}	.0181	sim = 7.06E-6	(-.0045; .0061)	<.0001
Pairwise P_{ST} (partial Mantel test)		$N = 28$	$r_M = .8626$.0004
Pairwise Π_{ST} (partial Mantel test)		$N = 28$	$r_M = .899$.0008
Mimicry structure:				
Global I_{ST}	.1541	sim = .0729	(.0564; .0938)	<.0001
Pairwise I_{ST} (partial Mantel test)		$N = 28$	$r_M = .8145$.0007
Association tests:				
Regression	-.0021	sim = 5.74E-6	(-.0004; .0004)	<.0001
Simulation	.2713	sim = .9838	(.8981; 1.0605)	<.0001
Incidence data set:				
Phylogenetic structure:				
Global Π_{ST}	.0168	sim = 2.6E-05	(-.0038; .0052)	<.0001
Pairwise Π_{ST} (partial Mantel test)		$N = 105$	$r_M = .8659$.0001
Mimicry structure:				
Global I_{ST}	.0617	sim = -.0048	(-.0102; .0017)	<.0001
Pairwise I_{ST} (partial Mantel test)		$N = 105$	$r_M = .9268$	<.0001
Association tests:				
Regression	-.0021	sim = -4.19E-6	(-.0004; .0004)	<.0001
Simulation	.2786	sim = .9813	(.8947; 1.0570)	<.0001

Note: Obs is the value of a metric measured on observed data, sim is the mean value of randomized or simulated metrics, the values between parentheses represent the 95% confidence interval (CI) of randomized or simulated metrics, N is the number of pairwise comparisons in partial Mantel tests between P_{ST} , Π_{ST} , or I_{ST} and altitudinal distances controlling for spatial distances, r_M is the Mantel correlation, and p is the p value of the test. All tests are significant after Bonferroni correction for multiple independent tests, except for the global P_{ST} in the abundance data set (adjusted values of α : 0.01 for global indexes and partial Mantel tests, 0.0125 for association tests).

dance data set, but this is not significant after Bonferroni correction (table 2). There is no relationship between either pairwise P_{ST} or Π_{ST} with spatial distance between pairs of communities (fig. 2A, 2B). Pairwise P_{ST} and Π_{ST} show a strong linear positive relationship with elevation distance between sites (fig. 2A, 2B). Partial Mantel tests confirm the positive relationship between pairwise P_{ST} or Π_{ST} with altitudinal distance independently of geographical distance (table 2; the relationship remains significant after Bonferroni correction).

Phylogenetic richness decreases linearly with altitude (fig. 3C), whereas the proportion of species in the four most diverse genera increases with altitude (fig. 3D). In both cases, the tests remain significant after Bonferroni correction for multiple independent tests (adjusted $\alpha = 0.0125$). Species richness and mimicry richness, however, show no clear relationship with altitude (fig. 3A, 3B, respectively).

Mimicry Structure

Comimetic species are significantly clustered within communities (mimicry clustering), indicated by the observation that global I_{ST} estimated from mimicry pattern abundances per communities was significantly higher than expected under random distribution of mimicry pattern. This result is the same for both the abundance and incidence data sets, even after Bonferroni correction for multiple independent tests (table 2). Similarly to P_{ST} and Π_{ST} , mimicry clustering is related to altitudinal distance between sites after accounting for spatial autocorrelation (table 2; fig. 2B). This is consistent with the altitudinal distribution of mimicry patterns across their distribution range (see app. D).

Phylogenetic Signal, Altitude, and Mimicry

The phylogenetic autocorrelogram shows that there is a phylogenetic signal in altitudinal niche and that this signal is within the 95% confidence interval of a Brownian model of evolution (fig. 4). For species that diverged since 0.015 relative time units, closely related species tend to occupy more similar altitudes than more distantly related species. The Mantel test's r_M between phylogenetic distances and mimicry distances is weak but highly significant (Mantel test: $N = 16110$; $r_M = 0.1718$; $p < .0001$), indicating that closely related species also tend to belong to the same mimicry complex (phylogenetic signal in mimicry patterns).

Both tests of association between mimicry structure and altitude indicate that the association remains significant even when phylogenetic signal is taken into account for the abundance and incidence data sets (table 2). In the

regression-based method, mean residuals between comimetic species are significantly lower than expected at random (table 2). In the simulation-based method, mean altitudinal distance between comimetic species (our measure of association between mimicry and altitude) is significantly lower than expected under a Brownian model of evolution (table 2). These results indicate that comimetic species tend to occur at the same altitudes more often than predicted by the phylogenetic signal in these traits alone.

Discussion

We find that ithomiine community composition is strongly associated with altitude. We also show that community composition is shaped by positive, mutualistic interactions among species.

Habitat Filtering by Altitude

The abundance data set of 8 communities and the larger presence/absence set of 15 communities both showed strong phylogenetic and mimicry clustering linked with altitude, which in the community phylogenetic framework (Webb et al. 2002) implies that altitudinal structuring is an important process. Higher altitudes showed increased clustering and therefore appear to act as a stronger filter. Many climatic variables are correlated with altitude—especially temperature and, to a lesser extent, moisture—and several recent macroecological studies have shown butterfly species and communities to be particularly dependent on both of these variables (e.g., Hawkins and DeVries 2009; Hawkins 2010). Hawkins (2010) suggested that temperature is a limiting factor in determining butterfly species richness in cooler, temperate regions. The physiological adaptations needed to colonize a new, higher altitudinal zone may therefore be important. In addition, most herbivorous insects, including ithomiines, are monophagous or oligophagous, and their distribution is therefore also closely tied to that of their host plant (Hodkinson 2005). Colonization of a new altitude may be particularly difficult but, once achieved, opens up opportunities for local diversification. Differences in the extent to which different groups of organisms are able to colonize new altitudes may therefore help to explain why some groups have diversified dramatically in montane regions and others have not. Here phylogenetic clustering and phylogenetic signal in altitude indicate that ithomiine lineages did not undergo significant adaptive radiation across altitudinal bands (which would have resulted in phylogenetic overdispersion) but instead diversified within altitudinal bands (Elias et al. 2009b). In Webb et al.'s (2002) framework, phylogenetic overdispersion could also reveal competition, if traits involved in resource use are con-

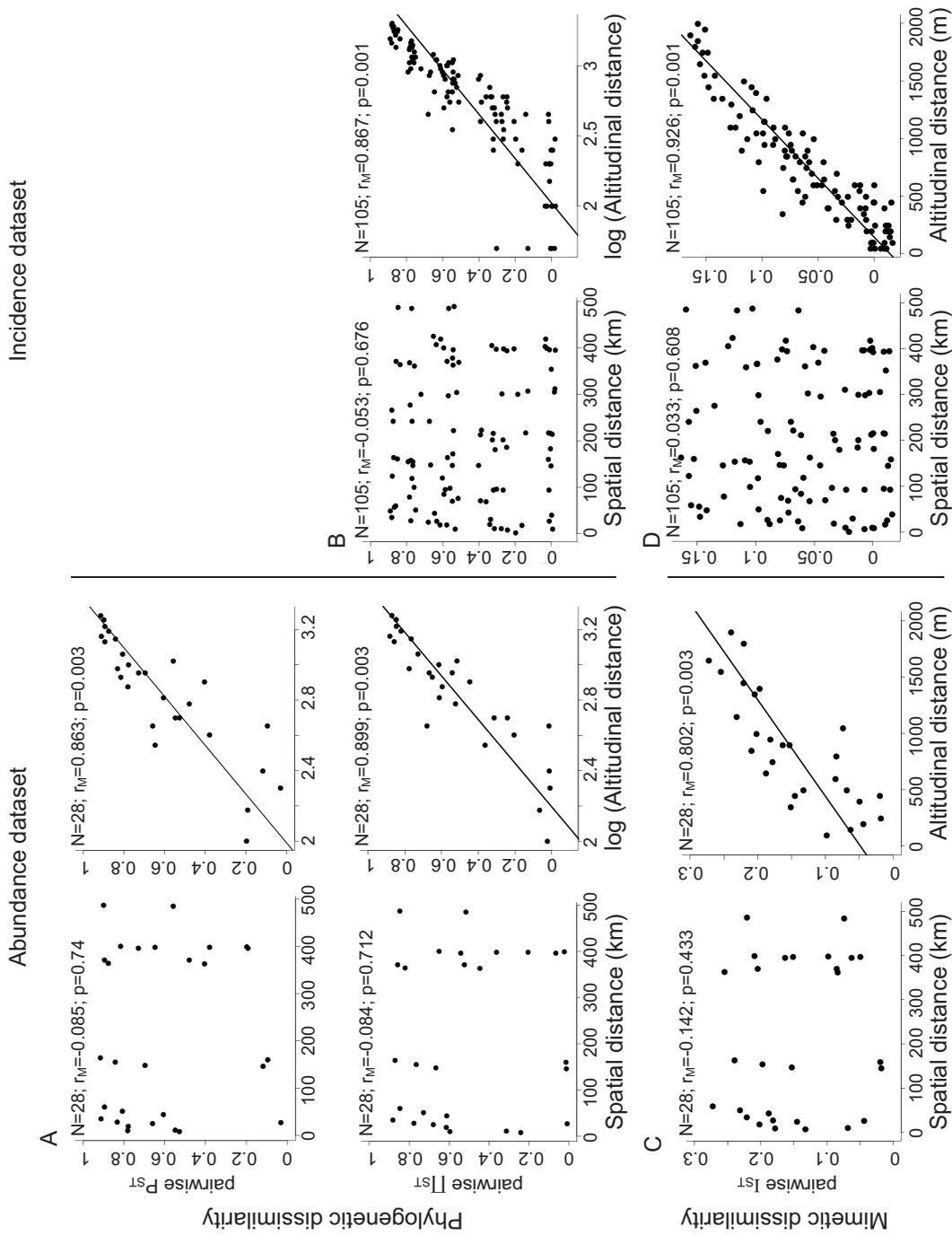


Figure 2: A, B, Relationships between phylogenetic dissimilarity and both spatial and altitudinal distances between pairs of communities, for the abundance data set and the incidence data set, respectively. Phylogenetic dissimilarity is measured by the P_{ST} index (*upper plots*) and the Π_{ST} index (*lower plots*). C, D, Relationships between mimicry dissimilarity and both spatial and altitudinal distances between pairs of communities, for the abundance data set and the incidence data set, respectively. Mimicry dissimilarity is measured by I_{ST} (Hardy and Senterre 2007) using the abundance of each mimetic pattern instead of species abundances. The results of Mantel tests are indicated for each graph.

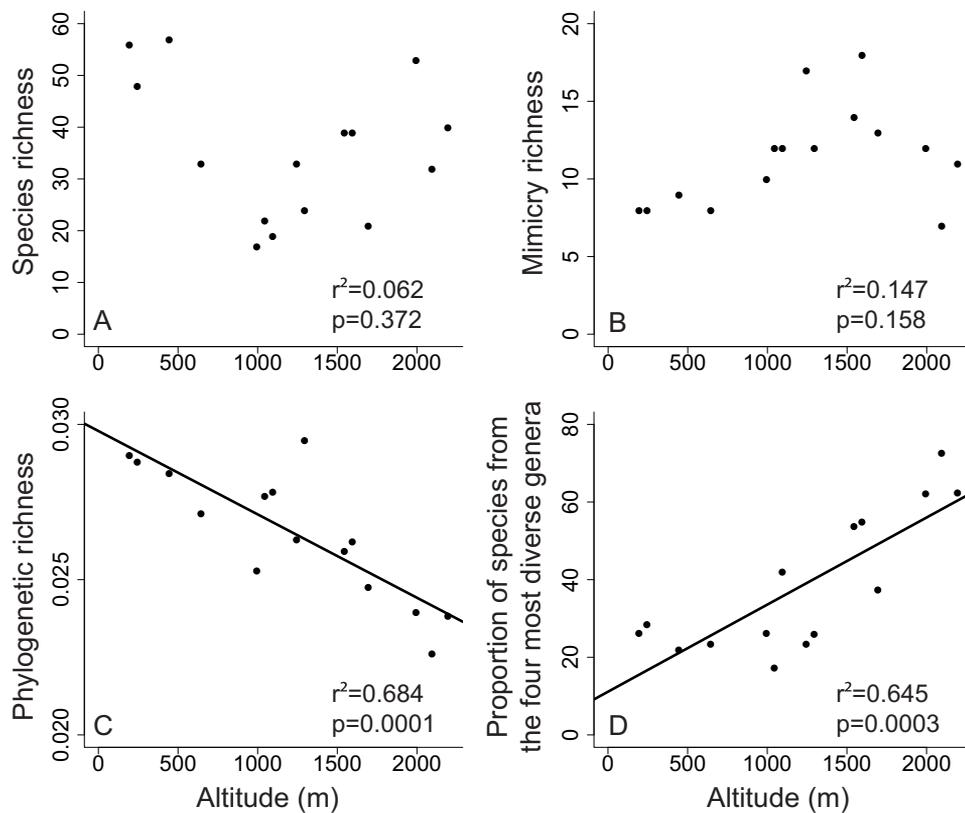


Figure 3: Relationships between altitude and species richness (A), mimicry richness (B), phylogenetic richness measured by the mean phylogenetic distances between species (C), and the percentage of all species in the community that belong to four-species-rich genera (D). Relationships were tested using linear regression (results indicated in each plot). The regression line is shown when the test is significant.

served. In this respect, data sets with information on relative abundances could be particularly informative if competition does not result in total exclusion of species but in reduced population size. In our case, no pattern of overdispersion was detected, indicating that competition has had a negligible impact on community structure in comparison with habitat filtering and mimicry. Competition might, however, act at smaller spatial scales; for example, a signature of competition was detected by Elias et al. (2008) within a lowland ithomiine community, but only between nonmimetic species. Assessing the phylogenetic structure of communities at similar altitudes might also shed light on whether competition plays an important role when the altitudinal filter is removed.

Surprisingly few studies have used Webb et al.'s (2002) community phylogenetic framework to understand biodiversity patterns along altitudinal gradients. Our study, in addition to studies of Andean hummingbirds (Graham et al. 2009), North American and European ants (Machac et al. 2011), and European alpine butterflies (Pellissier et al. 2013), found a pattern of increasing phylogenetic clustering at high altitudes. Rocky Mountain microbes (Bryant

et al. 2008) and tropical plants (Hardy and Senterre 2007) also proved to be phylogenetically clustered along the altitudinal gradient. Only Bryant et al.'s (2008) study of Rocky Mountain plants found the opposite, namely, phylogenetic overdispersion at high altitudes. Whether there are consistent differences in phylogenetic community structure across altitudinal gradients in plants and animals can be determined only by more studies of both groups. Nevertheless, differences in key traits such as dispersal ability and rates of diversification are likely to play a role in explaining variation in trends between groups, and perhaps between plants and animals. For example, high-altitude communities in organisms with high dispersal rates and low diversification rates may be more strongly composed of cold-adapted lineages originating from temperate regions at higher latitudes (e.g., Descimon 1986; Hall 2005). Such communities are likely to be composed of many lineages, with each containing relatively few species. By contrast, organisms with low dispersal rates but high diversification rates are more likely to colonize high-altitude habitats from adjacent altitudes and then diversify, leading to relatively few lineages with many closely related

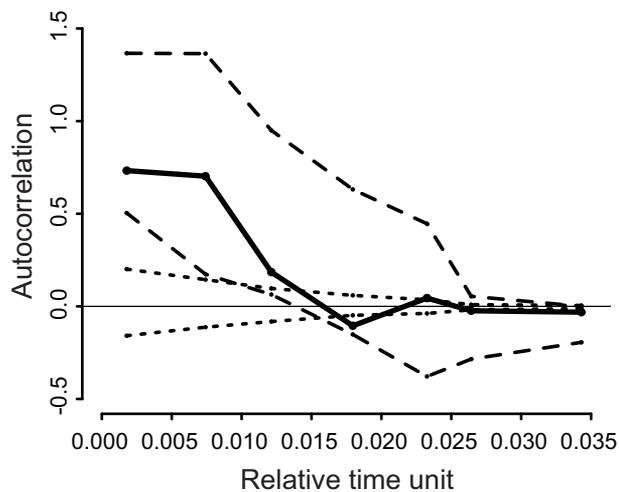


Figure 4: Phylogenetic autocorrelogram of altitude. For each divergence interval, the autocorrelation coefficient measures the similarity in altitude between pairs of species that diverged during this interval. The solid line represents the observed values, the dotted line represents the 95% confidence interval of values obtained under the hypothesis of no phylogenetic signal, and the dashed line represents the 95% confidence interval of values obtained under a Brownian model of evolution. Similarity in altitude between species decreases with divergent time between species. This pattern is consistent with a Brownian model of evolution.

species (e.g., Willmott et al. 2001). The latter pattern is what we found in this study. Indeed, ithomiine communities exhibit a clear decrease of phylogenetic diversity with altitude related to a decrease in the number of genera, with 70% of the species in the highest altitude communities occurring in only four genera. Machac et al. (2011) found a similar decrease in phylogenetic diversity associated with generic impoverishment in ants. This means that only a few lineages have been able to access and thrive at high altitudes.

Mimetic Interactions

As mentioned above, many climatic variables are correlated with altitude, and abiotic conditions undoubtedly play a major role in limiting species distribution. Biotic factors correlated with altitude, notably host plants of phytophagous insects, also limit species distribution. Here we find that mimicry acts as an additional biotic structuring process, and we suggest two ways in which it may do so. First, we find that different mimicry patterns dominate at different altitudes and that comimetic species tend to occur at similar altitudes. Consequently, altitudinal segregation of mimicry complexes is another factor that may act as a filter, constraining species' ranges by the distribution of their mimicry complex. Colonization of a different altitude

should therefore drive mimicry shifts, a likely cause of speciation (Jiggins 2008), and there is indeed evidence that changes in both altitude (Elias et al. 2009b) and color pattern (Jiggins et al. 2006) are associated with cladogenesis in ithomiine genera. Therefore, mimicry may have played a key role in the historical processes that have shaped current ithomiine communities. Second, we find that the sharing of similar altitudes in comimetic species is only partly due to phylogenetic signal in both color pattern and altitude, as the association between altitude and mimicry structures is stronger than expected based on the phylogenetic signal of these traits. Despite strong filtering by altitude, mutualistic interactions are therefore powerful enough to shape community structure. We hypothesize that mutualistic interactions reinforce comimetic species coexistence along the altitudinal gradient, probably by initial convergence in color pattern among coexisting species, followed by convergence in altitudinal niche of the newly comimetic species.

Implications for Response of Ecosystems in the Face of Climate Changes

Understanding and predicting the response of ecosystems to climate changes is one of the major challenges in ecology, particularly along ecological gradients. A number of studies have documented the influence of climate change in montane regions, pointing to the sensitivity of montane species and the likelihood of elevated risks of extinction to such species through climate change (Raxworthy et al. 2008; Chen et al. 2009; Sheldon et al. 2011). Recent studies have emphasized the importance of interactions between species in predictive models, as they play a major role in community structuring. However, most focus has been given to negative interactions such as trophic interactions or competition (Moorcroft et al. 2006; Araujo and Luoto 2007; Schweiger et al. 2008; Urban et al. 2012). Sheldon et al. (2011) recently proposed a model to predict the effect of a warming climate on 37 montane communities. They focused on how species co-occurrence, and therefore potential interactions, might be lost by such changes, leading to "community disassembly." Disassembly was highest in tropical montane communities, with up to 50% loss of co-occurrence for a shift of 5°C and dispersal proportional to altitudinal range. Community disassembly can clearly have a negative effect on some species by dislocating them from key resources but conversely may prove beneficial for at least some other species, for example, by relaxing predation or parasitism. However, when positive interactions among species are considered, the impact of community disassembly is likely to be more universally harmful. In the context of mimicry, varying rates of colonization of new altitudes in response to climate change may result

in no-analog communities (Urban et al. 2012) and assemblages of mimicry patterns that did not formerly coexist. If two comimetic species that initially coexisted fail to reach the same altitudinal range after climate warming—for instance, because of differences in dispersal capacities or in ecological tolerance—then both species will suffer increased predation as predicted by classical Müllerian mimicry theory (Müller 1879), with a concomitant increase in extinction probability. The powerful effect of mimicry in structuring tropical montane ithomiine communities is consistent with recent work suggesting that biological interactions are strong in the tropics (Schemske et al. 2009) and indicates that the loss of such positive interactions may result in even greater stress on such communities than predicted by Sheldon et al. (2011). Furthermore, due to their role as drivers of mimicry complexes involving other insect taxa (Beccaloni 1997a), disassembly of ithomiine communities is likely to have taxonomically far-reaching consequences.

Conclusion

Previous results have shown that positive interactions affect the structure of ithomiine species assemblages at fine spatial and ecological scales (microhabitat within a single community), driving adaptive ecological convergence among comimetic species (Elias et al. 2008). In this article, we demonstrate that mutualistic mimicry is powerful enough to drive adaptive community structure and ecological convergence at large spatial and ecological scales, where phylogenetic constraints on traits involved in niche adaptation are likely stronger. Ithomiine communities thus appear as tightly knit adaptive assemblages, resulting from a long history of coevolution concomitant with diversification in the Andes. Because of the ubiquity of positive interactions (Bshary and Noe 1997; Alexandrou et al. 2011), our results extend far beyond our study system. We argue that the community phylogenetic framework and, more generally, community ecology need to take into account positive interactions as a structuring process (Elias et al. 2009a) to better understand the factors underlying ecosystems and species assemblages and to predict ecosystem response to global changes.

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Some of the more than 150 ithomiine species that inhabit the eastern slopes of the Andes and show convergence in warning color pattern and elevation niche. *Left*, *Oleria onega* (left) and *Hyposcada illinissa* (right), which diverged 19 million years ago yet converged in wing patterns that advertise their unpalatability to predators (photo credit: Bigal River Biological Reserve, Ecuador). *Right*, *Oleria athalina* (photograph by M. Elias).