Taxon-dependent diversity response along a temperate elevation gradient covered by grassland (#89456)

First submission

Guidance from your Editor

Please submit by **19 Sep 2023** for the benefit of the authors (and your token reward) .

Structure and Criteria
Please read the 'Structure and Criteria' page for general guidance.

Custom checks
Make sure you include the custom checks shown below, in your review.

Raw data check
Review the raw data.

Image check
Check that figures and images have not been inappropriately manipulated.

If this article is published your review will be made public. You can choose whether to sign your review. If uploading a PDF please remove any identifiable information (if you want to remain anonymous).

Files

Download and review all files from the materials page.

3 Figure file(s)
1 Table file(s)
1 Other file(s)

Custom checks

Field study

Have you checked the authors field study permits?
Are the field study permits appropriate?

Structure and Criteria

2

Structure your review

The review form is divided into 5 sections. Please consider these when composing your review:

1. **BASIC REPORTING**
2. **EXPERIMENTAL DESIGN**
3. **VALIDITY OF THE FINDINGS**
4. General comments
5. Confidential notes to the editor

You can also annotate this PDF and upload it as part of your review

When ready submit online.

Editorial Criteria

Use these criteria points to structure your review. The full detailed editorial criteria is on your guidance page.

BASIC REPORTING

- ✓ Clear, unambiguous, professional English language used throughout.
- ✓ Intro & background to show context. Literature well referenced & relevant.
- ✓ Structure conforms to PeerJ standards, discipline norm, or improved for clarity.
- ✓ Figures are relevant, high quality, well labelled & described.
- ✓ Raw data supplied (see PeerJ policy).

EXPERIMENTAL DESIGN

- ✓ Original primary research within Scope of the journal.
- ✓ Research question well defined, relevant & meaningful. It is stated how the research fills an identified knowledge gap.
- ✓ Rigorous investigation performed to a high technical & ethical standard.
- ✓ Methods described with sufficient detail & information to replicate.

VALIDITY OF THE FINDINGS

- *i* Impact and novelty not assessed. *Meaningful* replication encouraged where rationale & benefit to literature is clearly stated.
- ✓ All underlying data have been provided; they are robust, statistically sound, & controlled.
- ✓ Conclusions are well stated, linked to original research question & limited to supporting results.

Standout reviewing tips

The best reviewers use these techniques

Tip	*Example*
Support criticisms with evidence from the text or from other sources	*Smith et al (J of Methodology, 2005, V3, pp 123) have shown that the analysis you use in Lines 241-250 is not the most appropriate for this situation. Please explain why you used this method.*
Give specific suggestions on how to improve the manuscript	*Your introduction needs more detail. I suggest that you improve the description at lines 57- 86 to provide more justification for your study (specifically, you should expand upon the knowledge gap being filled).*
Comment on language and grammar issues	*The English language should be improved to ensure that an international audience can clearly understand your text. Some examples where the language could be improved include lines 23, 77, 121, 128 – the current phrasing makes comprehension difficult. I suggest you have a colleague who is proficient in English and familiar with the subject matter review your manuscript, or contact a professional editing service.*
Organize by importance of the issues, and number your points	*1. Your most important issue* *2. The next most important item* *3. …* *4. The least important points*
Please provide constructive criticism, and avoid personal opinions	*I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC*
Comment on strengths (as well as weaknesses) of the manuscript	*I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.*

Taxon-dependent diversity response along a temperate elevation gradient covered by grassland

Santiago Santoandré Corresp., [1] , **Carolina Samanta Ramos** [1] , **Pablo Picca** [2] , **Julieta Filloy** [1]

[1] Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales (IEGEBA-CONICET), Universidad de Buenos Aires, Ciudad de Buenos Aires, Argentina
[2] Departamento de Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas y Naturales., Universidad de Buenos Aires, Ciudad de Buenos Aires, Argentina

Corresponding Author: Santiago Santoandré
Email address: santoandre@ege.fcen.uba.ar

Elevational gradients constitute excellent systems for understanding the mechanisms that generate and maintain global biodiversity patterns. The climatic gradient associated with elevation produces a sequence of different habitat types that influences the distribution of animal species. The study of the same habitat type along an elevation gradient is an ideal scenario to compare alternatives to the energy hypotheses. Our aim was to investigate how changes in climatic conditions along the elevational gradient drive α- and β-diversity of four taxa in a mountain system located within a grassland biome. We sampled ants, spiders, birds and plants, and measured climatic variables at six elevational bands (with 10 sampling sites each) established between 470 and 1000 masl on a mountain from the Ventania Mountain System, Argentina. Species richness per site and β-diversity (turnover and nestedness) between the lowest band and upper sites were estimated. To assess the response of β-diversity to elevation and each climatic variable we used generalized linear models (GLMs) and ranked climatic models following the Akaike information criterion. For most taxa, species richness declined at high elevations and energy, through temperature, was the major driver of species richness for ants and plants, and through productivity for birds, prevailing over water availability. The major β-diversity component was turnover for plants, spiders and birds, and nestedness for ants. The unique environmental conditions of the upper bands favoured the occurrence of specialist and endemic species. In high-elevation areas global climate warming may lead to biota homogenization through the loss of specialists and to an increase in species richness.

Taxon-dependent diversity response along a temperate elevation gradient covered by grassland

Santiago Santoandré[1], Carolina S. Ramos[1], Pablo Picca[2] and Julieta Filloy[1]

[1] Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires - IEGEBA (CONICET-UBA), Ciudad Universitaria, Pab 2, Piso 4, BAC1428EHA, Argentina.

[2] Departamento de Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina.

Corresponding Author and Submission admin:

Santiago Santoandré[1]

Intendente Güiraldes 2160 - Ciudad Autónoma de Buenos Aires, C1428EGA, Argentina.

Email address: santoandre@ege.fcen.uba.ar

Abstract

Elevational gradients constitute excellent systems for understanding the mechanisms that generate and maintain global biodiversity patterns. The climatic gradient associated with elevation produces a sequence of different habitat types that influences the distribution of animal species. The study of the same habitat type along an elevation gradient is an ideal scenario to compare alternatives to the energy hypotheses. Our aim was to investigate how changes in climatic conditions along the elevational gradient drive α- and β-diversity of four taxa in a mountain system located within a grassland biome. We sampled ants, spiders, birds and plants, and measured climatic variables at six elevational bands (with 10 sampling sites each) established between 470 and 1000 masl on a mountain from the Ventania Mountain System, Argentina. Species richness per site and β-diversity (turnover and nestedness) between the lowest band and upper sites were estimated. To assess the response of β-diversity to elevation and each climatic variable we used generalized linear models (GLMs) and ranked climatic models following the Akaike information criterion. For most taxa, species richness declined at high elevations and energy, through temperature, was the major driver of species richness for ants and plants, and through productivity for birds, prevailing over water availability. The major β-diversity component was turnover for plants, spiders and birds, and nestedness for ants. The unique environmental conditions of the upper bands favoured the occurrence of specialist and endemic species. In high-elevation areas global climate warming may lead to biota homogenization through the loss of specialists and to an increase in species richness.

Keywords

climatic drivers, energy hypothesis, mountain, multi-taxa, nestedness, turnover

Introduction

Life is heterogeneously distributed on Earth and the attributes of biological communities most often vary in space, giving rise to patterns. The study of the spatial or geographical processes underlying these patterns is a topical issue in ecology (Hawkins et al., 2003). In this regard, elevational gradients are considered valuable systems to better understand the mechanisms involved in their generation and maintenance (Lomolino, 2001; McCain, 2009; Peters et al., 2016; Ramos et al., 2021). Mountain gradients offer a variety of conditions useful to answer particular questions about diversity drivers (McCain, 2009; Sundqvist, Sanders & Wardle, 2013). In mountain systems temperature decreases with elevation while water availability depends on the context (McCain, 2009). In general, the climatic gradient associated with an increase in elevation creates a sequence of habitat types (i.e. steppe, forest and grassland). The structuring of animal communities is not only determined by climate but also by changes in habitat type, either directly through resource provision, or indirectly by modifying environmental conditions (i.e. soil temperature and humidity; (Werenkraut, Fergnani & Ruggiero, 2015). However, it is still unclear how climatic drivers affect diversity along elevational gradients with a single habitat type (e.g. grassland).

Species richness has been the most studied component of diversity along elevational gradients (McCain & Grytnes, 2010) and energy and water are known to be the main drivers of the geographical distribution and diversity patterns of species (Hawkins et al., 2003). An increase in incident energy favours an increase in taxonomic richness by providing support to species that otherwise would be limited by physiological constraints. On this basis, species richness in mountains is expected to decrease with decreasing temperature (Sanders et al., 2007). In animal communities, energy and water conditions may limit species richness by affecting the availability of trophic resources given by the productivity of the systems (Mittelbach et al., 2001). Temperature decreases monotonically with elevation, while water availability may decrease or increase and their combined effect results in different patterns of primary productivity (McCain, 2009). Changes in habitat type creates new niche opportunities for animal species and contributes to diversify the forms of environmental resource exploitation, thus increasing species diversity (Tews et al., 2004). Moreover, the fact that in most habitats plant communities determine the structure of the environment has a strong influence on the distribution of and interaction between animal species (Atauri, De Lucio & Lucio, 2001; Tews et al., 2004; Fergnani, Sackmann & Ruggiero, 2010). There is little information on the ~~combined~~ response of various taxa to environmental factors along an elevation gradient, and the few available studies have included different habitat types in the analyses (Peters et al., 2016; Di Nuzzo et al., 2021). An elevation gradient with a single habitat type is optimal for comparing variants of the energy hypotheses, and whether diversity patterns respond to a single main driver or depend on the taxon.

Changes in the species composition of communities (β-diversity) are crucial for understanding the causes of variation in spatial patterns of species distribution (Liira et al., 2008). It has been found that changes in the taxonomic composition of species may be associated with changes in environmental conditions or geographical distance (MacArthur, 1972; Hubbell, 2001). Association with changes in environmental factors provide evidence that differences in species composition are due to differences in the degree of species specialization for the different dimensions of their ecological niche (MacArthur, 1972), while association with geographical distance suggests species dispersal limitations (Condit et al., 2002). Therefore, the degree of taxonomic similarity between communities separated by a short geographical distance and in the absence of geographical barriers to dispersal will depend on the similarity of their environments and the species capacity to adapt to the environment (Qian, Ricklefs & White, 2005; Steinitz et al., 2006). Mountains are characterized by a high degree of environmental variation over a short geographical distance, making them an ideal setting to investigate changes in dissimilarity of species composition resulting from environmental changes (Jankowski et al., 2009; Tang et al., 2012). However, the relative contribution of the components of β-diversity (i.e. turnover and nestedness) to these changes remains unclear. In this regard, mountains with homogeneous habitat types provide an opportunity to explore changes in species composition due to other factors. A nested pattern is expected when a subset of generalist species found at lower elevations can support the environmental conditions at upper elevations, while a turnover pattern is likely to occur if species are specialists that only persist at higher elevations. Therefore, the analysis of the patterns of β-diversity components among assemblages allows us to delve deeper into the causes underlying changes in α-diversity along elevational gradients.

A multi-taxa approach is a promising method to elucidate complex community diversity patterns along elevational gradients (Peters et al., 2016; Di Nuzzo et al., 2021). Since assemblages composed of the same taxon tend to share many ecological niche characteristics, they are expected to respond similarly to environmental changes, giving rise to idiosyncratic responses. The multi-taxa approach involving phylogenetically distant taxa allows to reduce this effect. Indeed, broadening the taxonomic scope may lead to changes in some diversity patterns and reveals the importance of potential climate and environmental drivers of diversity (Di Nuzzo et al., 2021). Our aim was to investigate the effect of changes in climatic conditions on the diversity of four taxa (i.e. birds, ants, spiders, and plants) along an elevational gradient within a grassland biome.

Methods

Study area

The Ventania Mountain range is located at the southwest of Buenos Aires province, Argentina, in the Pampas plain. It is an isolated system characterized by steep slopes and a rugged terrain with numerous ravines, and the landscape is dominated by grasslands without trees or shrubs. This mountain system is ancient and dates back to 280-500 million years ago; it supports a rich biodiversity and a high level of endemism for several taxa (Kristensen & Frangi, 1995). Some examples of endemic vegetation are *Senecio ventanensis* (Asteraceae), *Poa iridifolia* (Poaceae), *Adiantum thalictroides* (Adiantaceae) and *Olsynium junceum* (Iridaceae) (Cuevas & Zalba, 2009). Moreover, a sun-spider species collected in the present study was described as a new species, *Gaucha casuhati* (Botero-Trujillo, Ott & Carvalho, 2017).

This study was conducted in the Ernesto Tornquist Provincial Park (38° 03′ 41″ S, 61° 59′ 18″ W) located in the centre of the Ventania System, which is one of the few conservation areas in the Pampean grasslands. Permission of Organismo Provincial para el Desarrollo Sostenible de la Provincia de Buenos Aires (number: 057/11). The peaks range from about 450 to 1,200 masl. The climate is temperate, with a mean annual temperature of 15°C and a mean annual rainfall of 700 mm (Kristensen & Frangi, 1995).

Study design

A series of six elevational bands were established covering the entire elevational gradient of the Ventana Mountain, from the valley at the foot of the mountain to near the top, separated by approximately 100 m of elevation (i.e. at average heights of 471, 517, 625, 723, 844 and 1001 masl). Fieldwork was carried out in spring and summer (mid-November to mid-January).

We used phylogenetically distant taxa: ants, spiders, birds and plants. These groups were selected because they have proven to be sensitive to environmental changes along elevational gradients, are very abundant and diverse, and provide fundamental ecosystem functions (Sekercioglu, 2012; Peters et al., 2016). Ants tend to exhibit high local diversity, performing numerous ecological functions in a wide variety of niches (Hölldobler & Wilson, 1990). They are thermophiles and their diversity tends to decrease at low temperatures (Hölldobler & Wilson, 1990; Sanders et al., 2007). Spiders are a ubiquitous component of invertebrate assemblages and important generalist predators in ecosystems (Wise, 1995). Their richness is associated with prey availability, which is often highly correlated with habitat structural complexity and primary productivity (Aisen et al., 2017). Birds are sensitive to alterations in vegetation structure (Phifer et al., 2017) and respond to changes in primary productivity along gradients (Harrower et al., 2017). Plants are sensitive to changes in abiotic conditions and provide habitat for animals, influencing their diversity and distribution (Nic Lughadha et al., 2005). Water and energy are crucial for plant physiological processes, thus having direct effects on plant diversity (O'Brien, 2006).

Sampling of ants and spiders and taxonomic identification

At each elevational band, we established ten sampling sites spaced at least 50 m apart and installed a pitfall trap at each sampling site, making up a total of 60 traps. Pitfall traps are widely used to obtain representative samples of ant and spider assemblages (Agosti et al., 2000; Pinto et al., 2018). These consisted of plastic containers (500 ml in volume and 85 mm in diameter) partially filled with a solution of 150 ml of propylene glycol: water (1:2) Traps were inserted flush with the ground surface and protected by a plastic cover to avoid flooding by rain. They remained open for three one-week periods. Captured specimens were identified to species level whenever possible or to morphospecies (hereafter referred to as species) based on diagnostic characters of the genera or families, using taxonomic keys and specialist consultations.

Bird survey

Birds were surveyed using the point-count method with a fixed 50-m radius (Ralph et al., 1996). At each elevational band, ten point-count sites were established ~~systematically~~ 150 m apart from each other. Surveys were conducted on clear and calm days, from dawn to the following 4 h. At each point-count site, we recorded all birds seen or heard over 5 min, except for birds flying overhead. The same two observers conducted all surveys.

Plant sampling and identification

Plant species were estimated using 1-m² and 12-m² quadrats for herbaceous plants and shrubs, respectively (Kent, 2012). This procedure was repeated twice near the point-count sites for birds (thus resulting in ten points per elevational band), and the species recorded in each subsample were pooled to obtain a species list by site. Plant species that could not be identified in the field were herborized for further identification in the laboratory. Plant taxonomy follows the Catálogo de Plantas Vasculares del Cono Sur and the online update (http://www.darwin.edu.ar).

Environmental gradient characterization

At each elevational band, an automatic sensor of temperature and relative humidity (HOBO U23002) was placed 10 cm above the ground level and gathered data at 6-h intervals for one month. Primary productivity was estimated at each level using a soil-adjusted vegetation index (SAVI) (Huete, 1988). SAVI maps covered the entire length of the elevational gradient and the average value for each elevational level was extracted. The maps were derived from Landsat-5 satellite images, taken in the springs of 2010 and 2011.

Data analyses

The trend of each environmental variable along the elevational gradient was described by a scatter plot as a function of elevation. Locally weighted regressions were fitted and trends were overlapped on the plots to visually analyze the elevational pattern of each environmental variable (Cleveland, Grosse & Shyu, 1993). These were fitted, by least squares with a span of 1.5, using the loess function of R software (Ramos et al., 2021). Then, species richness was calculated as the number of species of each taxon per sampling site. The elevational trend of species richness was analyzed using generalized linear models (GLMs) with this variable as a function of elevation. The distributions used were Poisson for total richness, ants, spiders and birds, and negative binomial for plants to avoid overdispersion (R, packages stats, glmmTMB and visreg). We used a model selection approach (Burnham & Anderson, 2002) to identify the main environmental factors driving changes in species richness along the elevational gradient. For each taxon, we ran GLMs with species richness as the response variable and each environmental variable as the independent variable, and ranked them following the Akaike information criterion (AIC) using the model.sel function of the R package MuMin (Barton et al., 2016). Models with a difference in AIC values less than two were considered equivalent to ~~the minimum AIC model~~ (Burnham & Anderson, 2002), and hence they were selected as the best set of models (Ramos et al., 2018).

Changes in species composition along the elevational gradient were estimated as taxonomic dissimilarity considering the turnover and nestedness components (Baselga, 2010). For each taxon, all species recorded at the sampling sites of the lowest elevational band were pooled. The change in species composition of the assemblages along the elevational gradient was estimated by comparing the dissimilarity at the lowest band with that recorded at each sampling site of the upper bands, based on species presence data (Santoandré et al., 2019). Finally, we compared patterns of taxonomic dissimilarity between taxa along the elevation gradient using a GLM with Beta distribution, since the dissimilarity values fell within the (0-1) interval (Ramos et al., 2018). We only compared the trends of the β-diversity components because the magnitude of the effect was influenced by data pooling.

Results

We identified a total of 176 plant species (1,417 presence records), 32 ant species (485), 48 spider species (206) and 31 bird species (236) collected and/or observed during samplings (Supplementary material). The environmental variables showed different elevational patterns: temperature (Fig. 1A) and SAVI (Fig. 1B) decreased with elevation, while relative humidity increased with elevation (Fig. 1C).

The regression analysis of changes in the species richness of ants, birds and plants along the elevation gradient showed a decreasing trend at hight elevations (ants: DF= 57, Chisq p-value= 2.822e-7; birds: DF= 58, Chisq p-value= 1.450e-7; plants: DF= 57, Chisq p-value= 1.312e-6) (Fig. 2). However, ants and plants richness showed a sharp decrease from the upper half of the elevational gradient onwards. On the other hand, spiders richness did not change significantly along the altitudinal gradient (DF= 56, Chisq, p-value = 0.378) (Fig. 2). Model selection analysis indicated that temperature was the main driver for the species richness pattern of ants and plants, and productivity for birds along the elevational gradient (Table 1).

Species composition showed an increase in total dissimilarity with elevation for ants (DF=47, Chisq p-value= 1.368e-8), spiders (DF= 47, Chisq p-value =9.001e-4), birds (DF=47, Chisq p-value= 5.910e-9) and plants (DF= 47, Chisq p-value = 1.890e-9) (Fig 3A). Species turnover increased with elevation in spiders (DF= 46, Chisq p-value= 9.657e-4), birds (DF= 47, Chisq p-value = 0.027) and plants (DF= 47, Chisq p-value 1.382e-12) (Fig 3B), but no significant trends were observed in ants (DF= 47, Chisq p-value = 0.554) (Fig 3). On the other hand, the nestedness component increased with elevation in ants (DF=47, Chisq p-value = 1.977e-9), but decreased with elevation in spiders (DF= 46, Chisq p-value=3.479e-4) and plants (DF= 47, Chisq p-value = 6.424e-9), while it showed no significant trends for birds (DF= 47, Chisq p-value= 0.801) (Fig 3C).

Discussion

Energy, primarily through temperature and productivity changes, were the major driver of species richness for most taxa, prevailing over water availability. The species richness of these taxa decreased at hight elevations and changes in species composition (β-diversity) were taxon-dependent. Thus, turnover was observed in plants, spiders and birds, and nestedness in ants. Despite the fact that upper elevations harboured lower species richness for most taxa, they provided suitable environmental conditions for species, including endemic ones, that were not found at the lowest sites. These results emphasize the key role played by this isolated and ancient mountain system in preserving regional biodiversity.

Temperature was the main environmental variable explaining the decreasing elevational richness pattern for ants and plants. This is in agreement with several elevational richness studies involving a single taxon in different habitat types and mountain contexts (McCain & Grytnes, 2010; Marathe et al., 2020). However, energy acting indirectly, via productivity, explained the decline in bird richness, as suggested by Harrower et al. (2017) for grassland songbird species. In our study, the absence of maximum productivity at intermediate elevations suggests that the Ventania System is composed of mountains with wet bases (McCain, 2007, 2009; Tellería, 2020). This may indicate that water availability was not a limiting factor, while energy had a different effect on species richness along the elevational gradient, possibly due to the similar responses across taxa to the thermal selection pressures and resources limitations that occur with increasing elevation. In the absence of environmental changes induced by habitat type change, energy availability overshadows the other factors (Harrower et al., 2017; Roeder, Roeder & Bujan, 2021).

The comparison of the species composition between the lowest band and each sampling site of the upper bands indicated that even though the taxonomic dissimilarity increased for all taxa, the main component of β-diversity differed among them. Thus, species turnover was the most important component for spiders, birds and plants, and species loss (nestedness) for ants. Species turnover has been reported as the major driver of changes in species composition along elevational gradients (Foord & Dippenaar-Schoeman, 2016; Gebrehiwot et al., 2019). Moreover, this component has been generally associated with changes in habitat type (Foord & Dippenaar-Schoeman, 2016; Aisen et al., 2017; Iijima & Morimoto, 2021). Our results show that species turnover may also occur within the same habitat type along an elevational gradient, probably due to the combined effect of two processes. First, climatic changes during the last millennia could have led to a latitudinal shift between the Patagonian (steppe), Espinal (xerophytic forest) and

Pampas (grassland) ecoregions. As a result, species from different ecoregions would have colonized the Ventania System at different historical times, and some of them could have persisted due to the high environmental heterogeneity of these mountains (Frangi & Bottino, 1995). Second, the speciation events that occurred in these ancient mountains most likely account for the presence of endemic species at different elevations (Cuevas & Zalba, 2009). The increase in nestedness of ant assemblages suggests that climatic factors at high elevations would have prevented many ant species present at the base from inhabiting upper elevations, where the extreme environmental conditions may not be compatible with their ecological niche. In conclusion, species with different abiotic requirements are expected to find suitable environmental conditions at different elevations. This process may result in turnover in species composition due to the presence of specialists (Marathe et al., 2021); or in nestedness when only a few base-dwelling generalist species can withstand the environmental conditions at upper elevations.

The taxa present in this ancient and isolated mountain system are expected to be differentially affected under the current global warming scenario (Barros et al., 2015). In this line of reasoning, ant richness would increase as a response to the relaxation of environmental filters that limit base species to ~~disperse to~~ upper elevations, while the diversity of plants, spiders, and birds would decrease due to the loss of species only found at upper elevations. The latter alternative could be due not only to the new unfavorable environmental conditions, but also to the competitive exclusion of lower elevation species over upper ones (Freeman, Strimas-Mackey & Miller, 2022). Mountain ecosystems are biodiversity hotspots especially threatened by global change (Löffler et al., 2011; Rahbek et al., 2019), because of the presence of species with small distribution areas and high levels of specialization (Viterbi et al., 2020). Finally, global warming may lead to biota homogenization in the Ventania Mountain System because it may promote a decrease in β-diversity and endemism but, at the same time, an increase in species richness.

Acknowledgements

We thank M. Apellaniz, H. Iuri, P. Berge, P. Cambiaggi and P. Pairo for field and lab assistance. The Organismo Provincial para el Desarrollo Sostenible of Buenos Aires Province gave permission and regulated the collection of ants, spiders and plants in the Ernesto Tornquist Provincial Park. Rangers of the Ernesto Tornquist Provincial Park provided logistic support.

References

Agosti D, Majer JD, Alonso LE, Schultz TR. 2000. *Ants standard methods for measuring and monitoring biodiversity*. Washington and London: Smithsonian Institution Press.

Aisen S, Werenkraut V, Márquez MEG, Ramírez MJ, Ruggiero A. 2017. Environmental heterogeneity, not distance, structures montane epigaeic spider assemblages in north-western Patagonia (Argentina). *Journal of Insect Conservation* 21:951–962. DOI: 10.1007/s10841-017-0034-8.

Atauri JA, De Lucio J V., Lucio V De. 2001. The role of landscape structure in species richness distribution of birds, amphibians, reptiles and lepidopterans in Mediterranean landscapes. *Landscape Ecology* 16:147–159. DOI: 10.1023/A:1011115921050.

Barros VR, Boninsegna JA, Camilloni IA, Chidiak M, Magrín GO, Rusticucci M. 2015. Climate change in Argentina: trends, projections, impacts and adaptation. *Wiley Interdisciplinary Reviews: Climate Change* 6:151–169. DOI: doi: 10.1002/wcc.316.

Barton PS, Sato CF, Kay GM, Florance D, Lindenmayer DB. 2016. Effects of environmental variation and livestock grazing on ant community structure in temperate eucalypt woodlands. *Insect Conservation and Diversity* 9:124–134. DOI: 10.1111/icad.12151.

Baselga A. 2010. Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* 19:134–143. DOI: 10.1111/j.1466-8238.2009.00490.x.

Botero-Trujillo R, Ott R, Carvalho LS. 2017. Systematic revision and phylogeny of the South American sun-spider genus Gaucha Mello-Leitão (Solifugae: Mummuciidae), with description of four new species and two new generic synonymies. *Staatliche Naturhistorische Sammlungen Dresden* 75:3–44.

Burnham KP, Anderson DR. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. New York: Springer. DOI: 10.1016/j.ecolmodel.2003.11.004.

Cleveland W, Grosse E, Shyu W. 1993. Chapter Local Regression Models of Statistical Models in S, edited by JM Chambers and TJ Hastie, 309–376.

Condit R, Pitman N, Leigh EG, Chave J, Terborgh J, Foster RB, Núñez PV, Aguilar S, Valencia R, Villa G, Muller-Landau HC, Losos E, Hubbell SP. 2002. Beta-diversity in tropical forest trees. *Science* 295:666–669. DOI: 10.1126/SCIENCE.1066854/SUPPL_FILE/CONDITWEBTABLE.XLS.

Cuevas YA, Zalba SM. 2009. Control de pinos invasores en el parque provincial ernesto tornquist (buenos aires): areas prioritarias y analisis de costos. *BioScriba* 2:76–89.

Fergnani PN, Sackmann P, Ruggiero A. 2010. Richness-environment relationships in epigaeic ants across the Subantarctic-Patagonian transition zone. *Insect Conservation and Diversity* 3:278–290. DOI: 10.1111/j.1752-4598.2010.00105.x.

Foord SH, Dippenaar-Schoeman AS. 2016. The effect of elevation and time on mountain spider diversity: a view of two aspects in the Cederberg mountains of South Africa. *Journal of Biogeography* 43:2354–2365. DOI: 10.1111/jbi.12817.

Frangi JL, Bottino OJ. 1995. Comunidades vegetales de la Sierra de la Ventana, Provincia de Buenos Aires, Argentina. *Revista de la Facultad de Agronomía* 71:93–133.

Freeman BG, Strimas-Mackey M, Miller ET. 2022. Interspecific competition limits bird species' ranges in tropical mountains. *Science* 377:416–420. DOI: 10.1126/SCIENCE.ABL7242.

Gebrehiwot K, Demissew S, Woldu Z, Fekadu M, Desalegn T, Teferi E. 2019. Elevational changes in vascular plants richness, diversity, and distribution pattern in Abune Yosef mountain range, Northern Ethiopia. *Plant Diversity* 41:220–228. DOI: 10.1016/J.PLD.2019.06.005.

Harrower WL, Srivastava DS, McCallum C, Fraser LH, Turkington R. 2017. Temperate grassland songbird species accumulate incrementally along a gradient of primary productivity. *PLoS ONE* 12:1–18. DOI: 10.1371/journal.pone.0186809.

Hawkins BA, Field R, Cornell H V., Currie DJ, Guégan JF, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Porter EE, Turner JRGG. 2003. Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84:3105–3117. DOI: 10.1890/03-8006.

Hölldobler B, Wilson E. 1990. *The ants*. Berlin, Heidelberg: Springer-Verlag. DOI: 10.1017/CBO9781107415324.004.

Hubbell SP. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press.

Huete AR. 1988. A soil-adjusted vegetation index (SAVI). *Remote Sensing of Environment* 25:295–309. DOI: 10.1016/0034-4257(88)90106-X.

Iijima D, Morimoto G. 2021. Bird community heterogeneity along four gradients of different orientations on a temperate mountain. *Ornithological Science* 20:65–82.

Jankowski JE, Ciecka AL, Meyer NY, Rabenold KN. 2009. Beta diversity along environmental gradients: implications of habitat specialization in tropical montane landscapes. *Journal of Animal Ecology* 78:315–327. DOI: 10.1111/J.1365-2656.2008.01487.X.

Kent M. 2012. *Vegetation description and data analysis: a practical approach*. Chichester, West Sussex, UK ; Hoboken, NJ: Wiley-Blackwell.

Kristensen MJ, Frangi JL. 1995. La sierra de la vantana: una isla de biodiversidad. *Ciencia Hoy* 5:25–34.

Liira J, Schmidt T, Aavik T, Arens P, Augenstein I, Bailey D, Billeter R, Bukáček R, Burel F, De Blust G, De Cock R, Dirksen J, Edwards PJ, Hamersky R, Herzog F, Klotz S, Kühn I, Le Coeur D, Miklová P, Roubalova M, Schweiger O, Smulders MJM, Van Wingerden WKRE, Bugter R, Zobel M. 2008. Plant functional group composition and large-scale species richness in European agricultural landscapes. *Journal of Vegetation Science* 19:3–14. DOI: 10.3170/2007-8-18308.

Löffler J, Anschlag K, Baker B, Finch O-D, Diekkrüger B, Wundram D, Schröder B, Pape R, Lundberg A. 2011. Mountain ecosystem reponse to global change. *Erdkunde* 65:189–213.

Lomolino MV. 2001. Elevation gradients of species-density: Historical and prospective views. *Global Ecology and Biogeography* 10:3–13. DOI: 10.1046/j.1466-822x.2001.00229.x.

MacArthur R. 1972. *Geographical Ecology: Patterns in the distribution of species*. New York: Harper & Row.

Marathe A, Priyadarsanan DR, Krishnaswamy J, Shanker K. 2020. Spatial and climatic variables independently drive elevational gradients in ant species richness in the Eastern Himalaya. *PLOS ONE* 15:e0227628. DOI: 10.1371/JOURNAL.PONE.0227628.

Marathe A, Shanker K, Krishnaswamy J, Priyadarsanan DR. 2021. Species and functional group composition of ant communities across an elevational gradient in the Eastern Himalaya. *Journal of Asia-Pacific Entomology* 24:1244–1250. DOI: 10.1016/J.ASPEN.2021.08.009.

McCain CM. 2007. Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Global Ecology and Biogeography* 16:1–13. DOI: 10.1111/J.1466-8238.2006.00263.X.

McCain CM. 2009. Global analysis of bird elevational diversity. *Global Ecology and Biogeography* 18:346–360. DOI: 10.1111/j.1466-8238.2008.00443.x.

McCain CM, Grytnes J. 2010. Elevational Gradients in Species Richness. *eLS*:1–10. DOI: 10.1002/9780470015902.a0022548.

Mittelbach GG, Steiner CF, Scheiner SM, Gross KL, Reynolds HL, Waide RB, Willig MR, Dodson SI, Gough L. 2001. What is the observed relationship between species richness and productivity? *Ecology* 82:2381–2396. DOI: 10.1890/0012-9658(2001)082[2381:WITORB]2.0.CO;2.

Nic Lughadha E, Baillie J, Barthlott W, Brummitt NA, Cheek MR, Farjon A, Govaerts R, Hardwick KA, Hilton-Taylor C, Meagher TR, Moat J, Mutke J, Paton AJ, Pleasants LJ, Savolainen V, Schatz GE, Smith P, Turner I, Wyse-Jackson P, Crane PR. 2005. Measuring the fate of plant diversity: towards a foundation for future monitoring and opportunities for urgent action. *Philosophical Transactions of the Royal Society B: Biological Sciences* 360:359–372. DOI: 10.1098/RSTB.2004.1596.

Di Nuzzo L, Vallese C, Benesperi R, Giordani P, Chiarucci A, Di Cecco V, Di Martino L, Di Musciano M, Gheza G, Lelli C, Spitale D, Nascimbene J. 2021. Contrasting multitaxon responses to climate change in Mediterranean mountains. *Scientific Reports 2021 11:1* 11:1–12. DOI: 10.1038/s41598-021-83866-x.

O'Brien EM. 2006. Biological relativity to water-energy dynamics. *Journal of Biogeography* 33:1868–1888. DOI: 10.1111/j.1365-2699.2006.01534.x.

Peters MK, Hemp A, Appelhans T, Behler C, Classen A, Detsch F, Ensslin A, Ferger SW, Frederiksen SB, Gebert F, Haas M, Helbig-Bonitz M, Hemp C, Kindeketa WJ, Mwangomo E, Ngereza C, Otte I, Röder J, Rutten G, Schellenberger Costa D, Tardanico J, Zancolli G, Deckert J, Eardley CD, Peters RS, Rödel MO, Schleuning M, Ssymank A, Kakengi V, Zhang J, Böhning-Gaese K, Brandl R, Kalko EKV, Kleyer M, Nauss T, Tschapka M, Fischer M, Steffan-Dewenter I. 2016. Predictors of elevational biodiversity gradients change from single taxa to the multi-taxa community level. *Nature Communications* 7. DOI: 10.1038/ncomms13736.

Phifer CC, Knowlton JL, Webster CR, Flaspohler DJ, Licata JA. 2017. Bird community responses to afforested eucalyptus plantations in the Argentine pampas. *Biodiversity and Conservation* 26:3073–3101. DOI: 10.1007/s10531-016-1126-6.

Pinto CM, Santoandré S, Zurita G, Bellocq MI, Filloy J. 2018. Conifer plantations in grassland and subtropical forest: Does spider diversity respond different to edge effect? *Journal of Forest Research* 00:1–7. DOI: 10.1080/13416979.2018.1506248.

Qian H, Ricklefs RE, White PS. 2005. Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. *Ecology Letters* 8:15–22. DOI: 10.1111/J.1461-0248.2004.00682.X.

Rahbek C, Borregaard MK, Colwell RK, Dalsgaard B, Holt BG, Morueta-Holme N, Nogues-Bravo D, Whittaker RJ, Fjeldså J. 2019. Humboldt's enigma: What causes global patterns of mountain biodiversity? *Science* 365:1108–1113. DOI: 10.1126/SCIENCE.AAX0149/ASSET/1BC19D96-73CF-4DE6-9877-1B5AF15DD26B/ASSETS/GRAPHIC/365_1108_F5.JPEG.

Ralph CJ, Geupel GR, Pyle P, Martin TE, DeSante DF, Milá B. 1996. *Manual de métodos de campo para el monitoreo de aves terrestres*. Albany, CA. DOI: 10.3145/epi.2006.jan.15.

Ramos CS, Isabel Bellocq M, Paris CI, Filloy J. 2018. Environmental drivers of ant species richness and composition across the Argentine Pampas grassland. *Austral Ecology* 43:424–434. DOI: 10.1111/aec.12579.

Ramos CS, Picca P, Pocco ME, Filloy J. 2021. Disentangling the role of environment in cross-taxon congruence of species richness along elevational gradients. *Scientific Reports* 11:1–11. DOI: 10.1038/s41598-021-83763-3.

Roeder KA, Roeder DV, Bujan J. 2021. Ant thermal tolerance: a review of methods, hypotheses, and sources of variation. *Annals of the Entomological Society of America* 114:459–469. DOI: 10.1093/aesa/saab018.

Sanders NJ, Lessard J, Fitzpatrick MC, Dunn RR. 2007. Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. *Global Ecology and Biogeography* 16:640–649. DOI: doi: 10.1111/j.1466-8238.2007.00316.x.

Santoandré S, Filloy J, Zurita GA, Bellocq MI. 2019. Taxonomic and functional beta diversity of ants along tree plantation chronosequences differ between contrasting biomes. *Basic and Applied Ecology* 41:1–12. DOI: 10.1016/j.baae.2019.08.004.

Sekercioglu CH. 2012. Bird functional diversity and ecosystem services in tropical forests, agroforests and agricultural areas. *Journal of Ornithology* 153:153–161. DOI: 10.1007/s10336-012-0869-4.

Steinitz O, Heller J, Tsoar A, Rotem D, Kadmon R. 2006. Environment, dispersal and patterns of species similarity. *Journal of Biogeography* 33:1044–1054. DOI: 10.1111/j.1365-2699.2006.01473.x.

Sundqvist MK, Sanders NJ, Wardle DA. 2013. Community and Ecosystem Responses to Elevational Gradients: Processes, Mechanisms, and Insights for Global Change. *Annual Review of Ecology, Evolution, and Systematics* 44:261–280. DOI: 10.1146/annurev-ecolsys-110512-135750.

Tang Z, Fang J, Chi X, Feng J, Liu Y, Shen Z, Wang X, Wang Z, Wu X, Zheng C, Gaston KJ. 2012. Patterns of plant beta-diversity along elevational and latitudinal gradients in mountain forests of China. *Ecography* 35:1083–1091. DOI: 10.1111/j.1600-0587.2012.06882.x.

Tellería JL. 2020. Long-term altitudinal change in bird richness in a Mediterranean mountain range: habitat shifts explain the trends. *Regional Environmental Change* 20. DOI: 10.1007/s10113-020-01657-y.

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F. 2004. Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. *Journal of Biogeography* 31:79–92. DOI: 10.1046/J.0305-0270.2003.00994.X.

Viterbi R, Cerrato C, Bionda R, Provenzale A. 2020. Effects of Temperature Rise on Multi-Taxa Distributions in Mountain Ecosystems. *Diversity 2020, Vol. 12, Page 210* 12:210. DOI: 10.3390/D12060210.

Werenkraut V, Fergnani PN, Ruggiero A. 2015. Ants at the edge: a sharp forest-steppe boundary influences the taxonomic and functional organization of ant species assemblages along elevational gradients in northwestern Patagonia (Argentina). *Biodiversity and Conservation* 24:287–308. DOI: 10.1007/s10531-014-0808-1.

Wise DH. 1995. *Spiders in ecological webs*. Cambridge: Cambridge University Press.

Table 1: Models that included temperature (temp) or productivity (SAVI) as the variable that best explained species richness for ants (ra), birds (rb) and plants (rp) along the elevation gradient of the Ventana Mountain, Buenos Aires province, Argentina. Species richness was explored using Generalized Linear Models (GLMs) with ln-link function. Only models with the lowest Akaike information criterion value are shown.

Figure 1. Elevational patterns of each environmental variable. The line was fitted to a local regression model with 95% confidence interval. Figure generated in R software (2023).

Figure 2: Species richness of the studied taxa (i.e. ants, spiders, birds and plants) along the elevational gradient of the Ventana Mountain, Buenos Aires province, Argentina. Lines indicate

the generalized linear model (GLM) for each taxon, with 95% confidence interval. Dots indicate the species richness at each sampling site. Points were jittered to avoid overlap.

Figure 3: Taxonomic dissimilarity and its components between the lowest altitudinal band and each sampling site of the upper bands. Lines indicate the generalized linear model (GLM) for each taxon, using Beta distribution with 95% confidence interval. The x-axis indicates the elevation (masl) of each upper band.

Table 1(on next page)

Table 1

Models that included temperature (temp) or productivity (SAVI) as the variable that best explained species richness for ants (ra), birds (rb) and plants (rp) along the elevation gradient of the Ventana Mountain, Buenos Aires province, Argentina. Species richness was explored using Generalized Linear Models (GLMs) with ln-link function. Only models with the lowest Akaike information criterion value are shown.

Model	AIC	w(AIC)
ra = e^(0.208 * temp - 2.342)	284	0.76
rb = e^(5.409 * SAVI – 0.113)	215	0.99
rp = e^(0.207 * temp – 1.254)	434	1.00

AIC: Akaike information criterion; rounded Akaike weight: w(AIC).

Figure 1

Figure 1

Elevational patterns of each environmental variable. The line was fitted to a local regression model with 95% confidence interval. Figure generated in R software (2023).

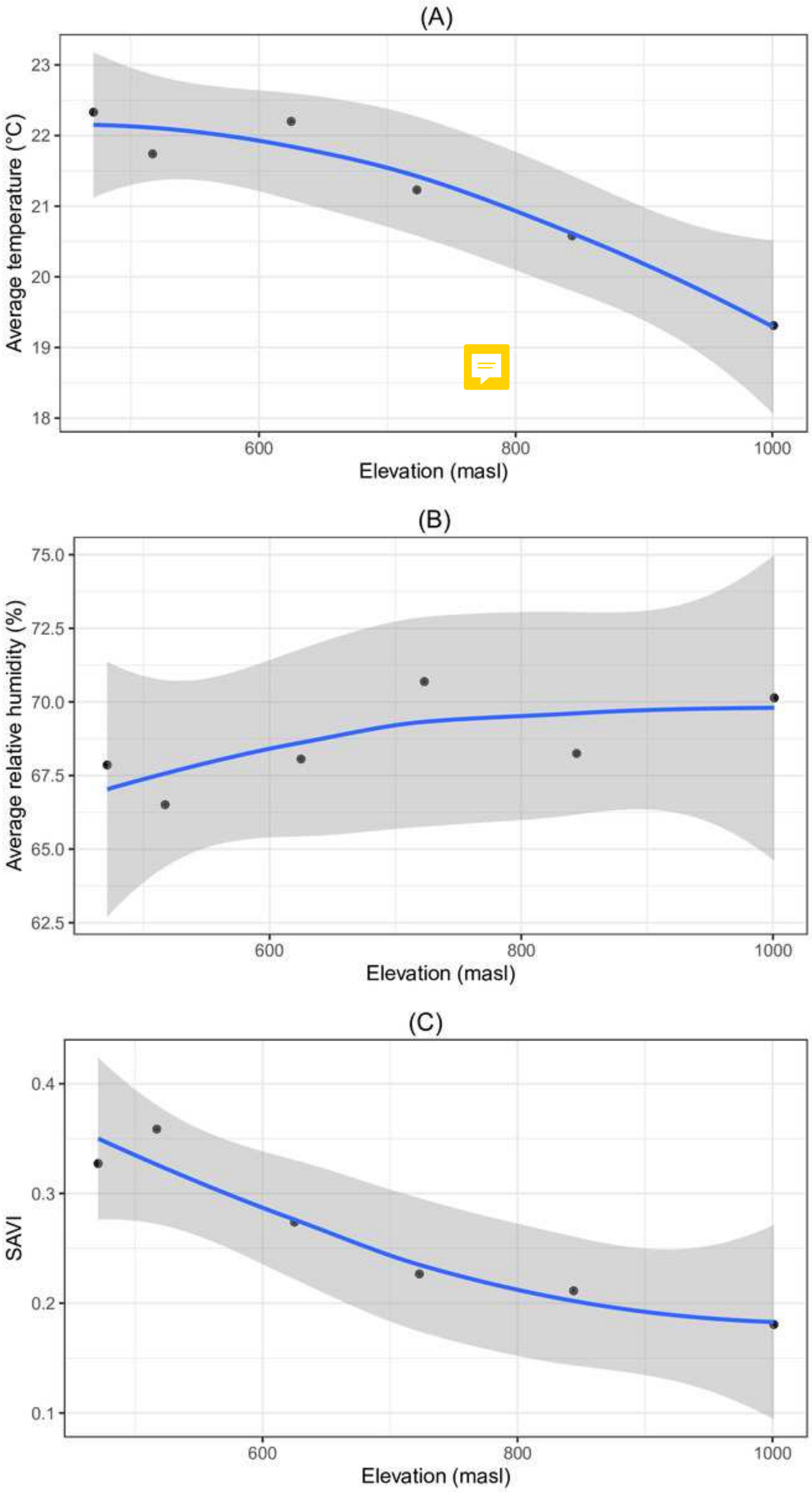

(A)
Average temperature (°C)
23
22
21
20
19
18
600
800
1000
Elevation (masl)
(B)
Average relative humidity (%)
75.0
72.5
70.0
67.5
65.0
62.5
600
800
1000
Elevation (masl)
(C)
SAVI
0.4
0.3
0.2
0.1
600
800
1000
Elevation (masl)

Figure 2

Figure 2

Species richness of the studied taxa (i.e. ants, spiders, birds and plants) along the elevational gradient of the Ventana Mountain, Buenos Aires province, Argentina. Lines indicate the generalized linear model (GLM) for each taxon, with 95% confidence interval. Dots indicate the species richness at each sampling site. Points were jittered to avoid overlap.

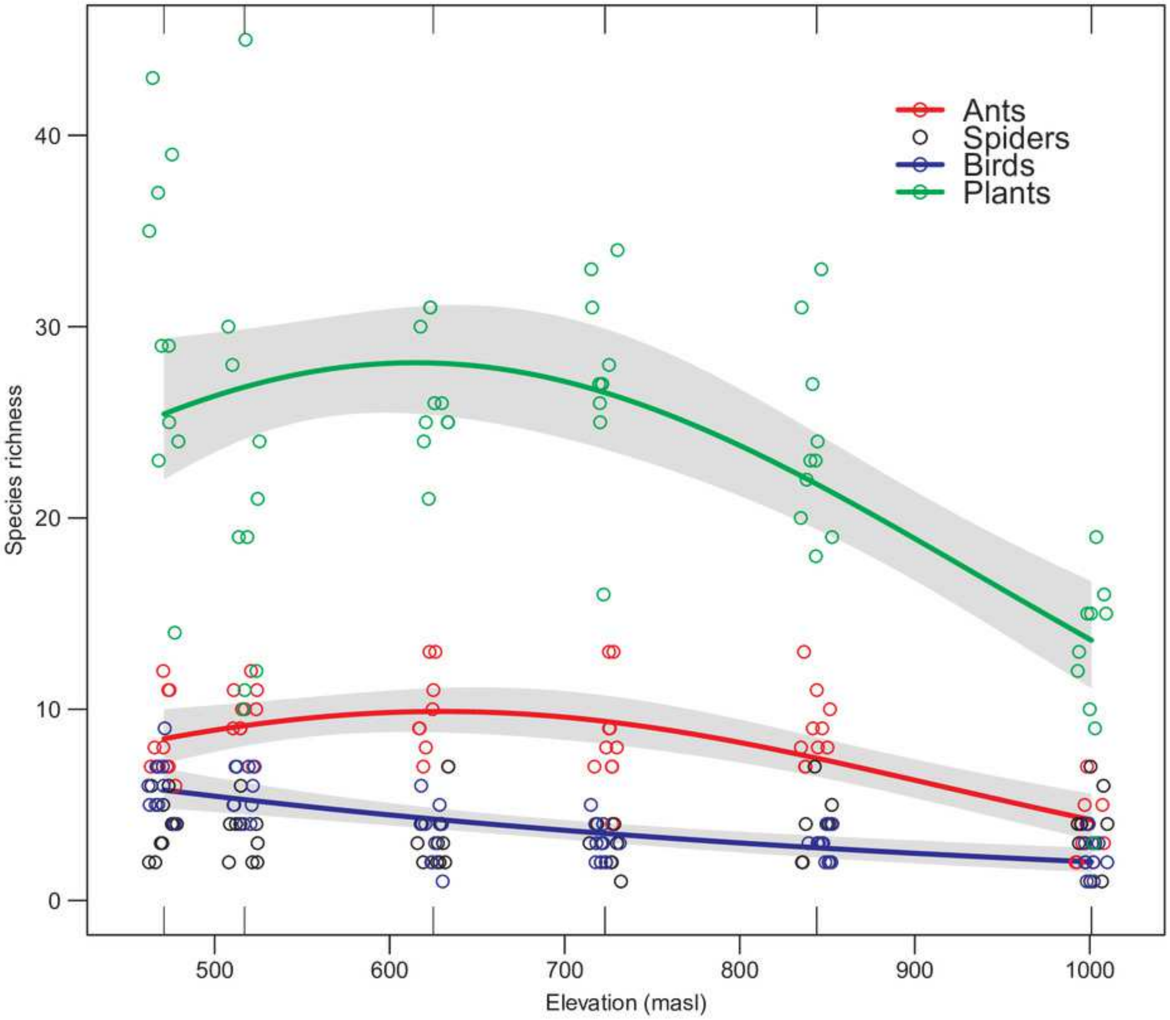
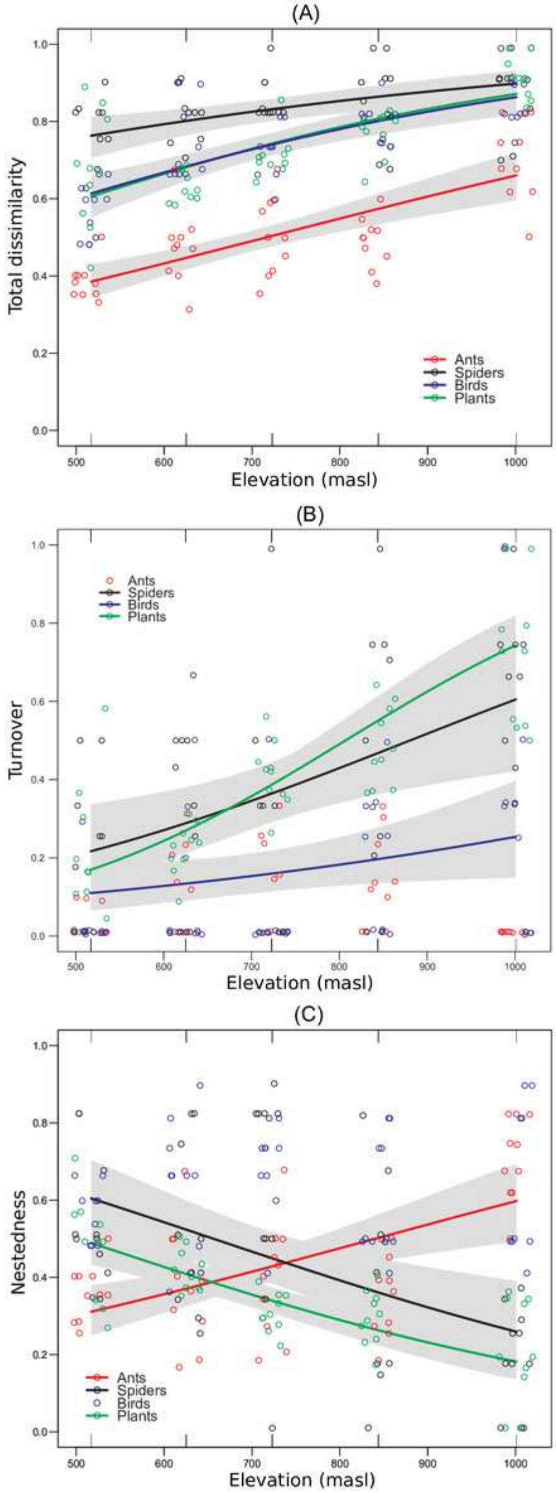

Ants
Spiders
Birds
Plants
Species richness
0
10
20
30
40
500
600
700
800
900
1000
Elevation (masl)

Figure 3

Figure 3

Taxonomic dissimilarity and its components between the lowest altitudinal band and each sampling site of the upper bands. Lines indicate the generalized linear model (GLM) for each taxon, using Beta distribution with 95% confidence interval. The x-axis indicates the elevation (masl) of each upper band.


(A)
Total dissimilarity
1.0
0.8
0.6
0.4
0.2
0.0
Ants
Spiders
Birds
Plants
500
600
700
800
900
1000
Elevation (masl)
(B)
Turnover
1.0
0.8
0.6
0.4
0.2
0.0
Ants
Spiders
Birds
Plants
500
600
700
800
900
1000
Elevation (masl)
(C)
Nestedness
1.0
0.8
0.6
0.4
0.2
0.0
Ants
Spiders
Birds
Plants
500
600
700
800
900
1000
Elevation (masl)