Altitudinal differences in alpha, beta and functional diversity of an amphibian community in a biodiversity hotspot

Jaime Villacampa a,b, Andrew Whitworth a,c,d, Laura Allen e and Juan E. Malo a,e

ABSTRACT
Biodiversity research along altitudinal gradients can provide us with new insights into conservation and human impacts. In this context, amphibians are a useful and important group due to their rapid response to environmental changes, severely threatened status and because of the gaps in our knowledge of their ecology, especially in tropical forests. Here, we investigate the differences in amphibian communities along an altitudinal gradient with the aim to understand how different groups respond to altitude and what factors drive such responses. We carried out our research in the Piñi-Piñi range, located in the Manu Biosphere Reserve (south-eastern Peru), a global biodiversity hotspot. We evaluated the changes in abundance, alpha, beta and functional diversity of the community with altitude along transects from 450 to 1150 m asl. We categorized species into functional groups based on their breeding sites, habitat and weight. Alpha diversity for the overall community decreased with increasing altitude, a trend partially driven by the absence of aquatic habitats in the higher elevations, which prevents colonisation by pond and stream breeders. Community composition changed with altitude and there was a low similarity between lower and higher elevations. Upper elevations were less diverse but contained species found nowhere else along the gradient, increasing the diversity of the range. Functional groups responded to altitude in different ways and several groups were absent or almost absent from the upper elevations: large species (>10 g), terrestrial, arboreal, and pond and stream breeders. Pond and stream breeders and those species found exclusively in the higher areas of the range are likely more vulnerable to habitat and climate change. Investigating the response of different functional groups and using multiple measures of diversity was useful for generating a detailed understanding of the changes in the community with altitude and their ecological and conservation implications.

RESUMEN
La investigación en biodiversidad en gradientes altitudinales puede proveernos de nuevas perspectivas sobre conservación e impactos humanos. En este contexto, los anfibios son un grupo importante y útil debido a su rápida respuesta a cambios ambientales, su grave estado de amenaza y por las lagunas en nuestro conocimiento de su ecología, especialmente en bosques tropicales. Aquí, investigamos las diferencias en las comunidades de anfibios a lo largo de un gradiente altitudinal con el objetivo de comprender cómo diferentes grupos responden a la altitud y qué factores llevan a estas respuestas. Llevamos a cabo nuestra investigación en la cordillera del Piñi-Piñi situada en la Reserva de la Biosfera del Manu (sudeste de Perú), un punto caliente de biodiversidad a nivel mundial. Evaluamos los cambios de la comunidad con la altitud en abundancia y diversidad alfa, beta y funcional a lo largo de transectos desde los 450 a los 1150 msnm. Categorizamos a las especies en grupos funcionales basados en sus hábitats reproductivos, hábitats y peso. La diversidad alfa para toda la comunidad disminuyó con el aumento de altura, una tendencia parcialmente causada por la ausencia de hábitats acuáticos en las zonas más altas lo que impide su colonización por especies que se reproducen en charcas y arroyos. La composición de la comunidad cambió con la altitud y la similitud entre las elevaciones altas y bajas fue baja. Las elevaciones superiores resultaron ser menos diversas pero albergaron especies que no se encontraron en ninguna otra parte del gradiente, aumentando la diversidad de la cordillera. Los grupos funcionales respondieron a la altitud de diferentes maneras y varios grupos no se encontraron o apenas se encontraron en las elevaciones superiores: especies grandes (>10 g), terrestres, arbóreas, y reproductores en charcas y arroyos. Los reproductores en charcas y arroyos y las especies que solo se encontraron en las zonas altas de la cordillera son probablemente más vulnerables a los cambios de hábitat y al cambio climático. Investigar la respuesta de los grupos funcionales y usar varias medidas de diversidad fue útil para generar un entendimiento más detallado de los cambios en la comunidad con la altitud y sus implicaciones ecológicas y para la conservación.

CONTACT Jaime Villacampa jaime.villacampa@hotmail.com

Supplemental data for this article can be accessed here.

© 2019 The Author(s). Published by Informa UK Limited, trading as Taylor & Francis Group. This is an Open Access article distributed under the terms of the Creative Commons Attribution License (http://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.
Introduction

Altitudinal gradient research provides us with new insights about biodiversity patterns and the potential responses of biodiversity to habitat change and climate change [1]. This is because humidity, temperature and UV radiation, amongst other biotic and abiotic factors, vary synergistically with elevation [2], thus creating natural laboratories in which to carry out biodiversity assessments. Research on tropical altitudinal gradients is of particular interest due to the extreme biodiversity held within them [1] and the high levels of micro-endemism, as a result of the narrow thermal niches of many species, which help generate a high community turnover within a small area [3,4].

Tropical montane forests are of great importance for biodiversity conservation and are highly vulnerable, yet we still know little of the biodiversity they contain [5,6]. The greatest human impacts on biodiversity globally are expected to be within tropical montane ecosystems [7,8], causing species extinctions and an extreme turnover of species [5,9]. The biggest threats to these areas are habitat loss and climate change [5,7]. Our knowledge of the impacts of these threats is hampered by the lack of a clear understanding of how communities and species respond to altitude. Assessments to date describe conflicting responses of the diversity and abundance of animal communities in relation to increasing altitude, including decreases [3,10], increases [11,12], and mid-peak responses [13,14]. The main difficulty is that many other factors act together with altitude [15,16] making it problematic to unravel the role of each factor and the synergies between them. One potential approach to solve this issue is to divide the overall community into functional groups based on morphological or ecological traits. Functional groups respond divergently to environmental change [17,18], which can help investigating the ecological drivers for observed patterns [19,20].

Amphibians are an ideal study group to investigate species’ responses to altitude due to their ectothermy, reduced mobility, limited dispersal capacity and narrow ecological requirements [21]. The large variations in life history within amphibians [22] allow us to understand the responses of species with different functional traits and use them to understand the responses of the overall community to altitude. Furthermore, amphibian diversity is highest in the tropics where they are highly threatened [23], while their ecology remains poorly studied [24,25]. However, even with the limited information available on tropical amphibians, population declines are well documented: habitat loss, habitat degradation and disease are the predominant causes [25–27] with climate change exacerbating the severity of these [28].

Here, we present a detailed study of the diversity and structure of a community of amphibians along an altitudinal gradient in the Andean foothills. We do so in one of the world’s most biodiverse and important conservation areas, the Manu Biosphere Reserve, a UNESCO World Heritage Site designated to protect the globally important Amazon rainforest and its biodiversity [29]. Through the assessment of functional groups and a fine-scale study approach, we aim to: i) assess species, functional group and community responses to altitude; and using this information ii) understand the conservation implications of these results, and iii) investigate what other factors are playing a role in the diversity and community composition differences with altitude.

Methods

Study site

The study was carried out in the reserve of the Manu Learning Centre research station (71°23′28.06″W, 12°47′21.849″S, 460 m asl), located in the Manu Biosphere Reserve (southeast Peru), the most diverse area in the world for amphibians [30]. Mean annual rainfall is approximately 4900 mm and the mean annual temperature is 24.2 °C (measured at the research station). The reserve is halfway between the cloud forest and lowland rainforest, located in a foothill area that has so far received little attention from biodiversity researchers, especially in relation to amphibians. Research on amphibians at the Manu Learning Centre has been carried out for over 6 years, with 71 species of amphibians recorded to date [31–33]. The altitudinal gradient is situated in the Piñi-Piñi mountain range. It covers a straight-line distance of 4 km that spans from the lowest areas next to the bank of the Alto Madre de Dios River (~450 m asl) to the peaks of the range (~1200 m asl). The study area is covered by low disturbance tropical forest. The Piñi-Piñi’s hydrological system is characterized in the lowlands by a few wide, fast-moving, permanent streams with numerous small, low-flowing creeks and several semi-permanent ponds. In the upper slopes, the streams are very infrequent, small and seasonal, and there are no ponds. The upper elevations of the range are very often covered by clouds.

Sampling methodology

Data collection was carried out during a three-month period in the 2013 dry season, from mid-June to mid-September. Four altitudinal bands were defined: 450–550, 650–750, 850–950 and 1050–1150 m asl, and ten 100 m long linear transects were marked in each band, giving a total of 40 transect sampling locations. Visual encounter surveys were carried out along the transects, and away from main trails to avoid known biases in surveying amphibians along trails [34]. This
method is especially effective for detecting the most common amphibian groups found within the study site and for representing as wide an array of the community as possible [35]. At the beginning of the study, a narrow path along each transect was lightly cut to facilitate surveys. After this, transects were left for at least a week before sampling to avoid any bias due to the disturbance. Transects did not include areas near streams, in order to avoid edge effects and to focus upon forest interior species. The starting points of the transects were separated by at least 50 m and adjacent transects ran in opposite directions. Each transect was surveyed five times, with at least 2 weeks between each repetition. Surveys were carried out at night, between 19:00 and 01:00, as most species in the study region are nocturnal. We recorded every amphibian detected within a 2 m band either side of the transect line and up to 3 m high. Transects were walked at a standardized pace of 25 to 30 min per 100 m. Surveys were carried out by teams of two or three observers, each led by an experienced herpetologist accompanied by one or two trained volunteers. All individuals detected during the sampling were identified in the field where possible [31,36–38].

Forest vegetation structure was recorded to evaluate the change in habitat features along the gradient. Along each transect, a 5 × 5 m plot was established every 20 m after the surveys finished. In each vegetation plot, the following data were recorded: canopy height and cover, understory density, number of trees with a diameter at breast height greater than 10 cm, leaf litter depth, abundance of epiphytes, fern cover, abundance of coarse woody debris and slope.

**Data analysis**

We conducted all our data analysis in R version 3.5.2 [39] and the code and datasets can be found in this GitHub repository: https://github.com/jvillacampa/amphibians-pini.

To explore the differences in environment along the altitudinal gradient we ran a principal component analysis based on the forest structure data at transect scale. This analysis was carried out using the R package vegan [40].

Species recorded during the study were classified into different functional groups based on traits of their natural history (Supplementary information 1, including literature used). The three traits were:

- Reproductive habitat: pond/stream breeders or others.
- Habitat: arboreal, terrestrial or semi-arboreal. Examples of semi-arboreal species are most *Pristimantis* species in this area, which can be found resting on the ground during the day and climb small trees and bushes during the night.
- Maximum weight recorded. We classified species depending on the maximum adult weight recorded: less than 2.5 g, between 2.5 and 10 g, and more than 10 g. These categories were chosen with the aim of splitting the community into small, medium and large species, based on the range of sizes commonly encountered.

We calculated alpha diversity for each altitudinal band and for each transect using Hill numbers (Hill, 1973): observed richness, Shannon entropy and Simpson diversity, using the R package iNEXT [41]. We also calculated the observed richness for each functional group. To compare observed richness between altitudinal bands, we created species accumulation curves for each band. We extrapolated observed richness to a standard sample size (n = 132); equivalent to double the smallest sample, the maximum that can be reliably extrapolated [42]. Abundances were calculated for each altitudinal band, functional group and species.

We tested the differences between bands in abundance, observed richness, Shannon and Simpson diversity through a series of models using the packages Stats [39] and Hmisc [43] in R. For abundance and richness, we used Poisson regressions and for Shannon and Simpson diversity we used linear regressions with a log response variable. We also modelled the differences in observed richness and abundance for most of the functional groups, except for those where the sample size was too low: pond/stream breeders, arboreal and species over 10 g.

To understand the changes in beta diversity we analysed the similarity between the amphibian communities of each band using the Chao-Jaccard estimated abundance-based similarity index using the R package vegan. We chose this index as it works well for small samples with numerous rare and unsampled species [44]. We also assessed the partitioning of beta diversity into the relative contributions of richness differences and species turnover along the gradient, using the beta.div.comp function of adespatial [45] with the quantitative Jaccard family of coefficients.

*Pristimantis reichlei* Padial and De la Riva, 2009 posed a challenge for accurate identification in the absence of genetic analysis, with two species potentially masquerading under this name. As this was one of the most common species in the area, we ran our community similarity analysis twice, once considering it as a single species and a secondly considering it as two separate species (Supplementary information 5). Both analyses showed the same pattern and we present the results considering them separate species.

**Results**

In total, 337 amphibians of 22 species were encountered after an accumulated sampling effort of 209 observer-
Altitudinal bands were segregated ecologically as shown by a principal component analysis run on environmental data collected along the gradient (Figure 1, Supplementary information 3-4). Transects at upper elevations were characterized by a higher abundance of ferns and epiphytes, deeper leaf litter and steeper slopes, whereas lower elevation sites had higher canopies, more canopy cover and denser understory vegetation.

Alpha diversity for the overall community was highest in the lower bands and decreased with altitude for all measures calculated: observed richness (Figure 2, Supplementary information 6; e.g. species richness differences between 450–550 and 1050–1150: \( p = 0.002 \), estimated coefficient = −0.75), Shannon and Simpson diversity (Figure 3, Supplementary information 6). Shannon and Simpson diversity was more sensitive for detecting differences between bands than species richness, which indicates a decrease in the evenness of the community with altitude. Overall abundance was lowest in higher altitudinal bands (Figure 3) but the only significant difference (at \( \alpha = 0.05 \)) was between the 650–750 m band and the two highest bands (Supplementary information 6; 650–750 and 850–950: \( p = 0.019 \), estimated coefficient = −0.35; 650–750 and 1050–1150: \( p = 0.002 \), estimated coefficient = −0.49).

Similarity in species composition showed a gradual change in the composition of amphibian communities with altitude and a marked separation between upper and lower bands (Table 1). The low similarity (9%) between the 450–550 m and the 1050–1150 m bands indicates a high turnover in the species composition along the gradient, a dissimilar community composition and a lack of nestedness. This is supported by the results...
of the beta diversity partitioning, which found that 23% of the beta diversity along the gradient was due to a change in richness and 77% due to species turnover.

Species richness patterns varied between functional groups (Figure 4, Supplementary information 6). Stream and pond breeders were absent from the upper bands, while for the group using other reproductive habitats there was only a difference in richness when comparing the lower two bands against the top band (both comparisons: $p = 0.02$, estimated coefficient = $-0.06$). Richness of species $< 2.5$ g decreased with altitude, although differences were only significant when compared against the top band ($450–550$ and $1050–1150$: $p = 0.001$, estimated coefficient = $-0.124$; $650–750$ and $1050–1150$: $p = 0.002$, estimated coefficient = $-1.17$; $850–950$ and $1050–1150$: $p = 0.024$, estimated coefficient = $-0.89$). The richness of species weighing between $2.5$ and $10$ g did not show any clear trend, although the top band had a higher richness than the rest, but this was only significantly different when compared against the $850–950$ band ($p = 0.002$, estimated coefficient = $0.92$). Very few individuals of species $> 10$ g were recorded, which prevented us from modelling their responses, but this group was nearly absent from the upper bands. Terrestrial species richness appeared to decrease with altitude, with a significant difference in richness between the lower bands and $850–950$ m ($450–550$ and $850–950$: $p = 0.022$, estimated coefficient = $-2.4$; $650–750$ and $850–950$: $p = 0.037$, estimated coefficient = $-2.2$). Semi-arboreal species richness tended to decrease with altitude and the differences were significant between the top band and the lower bands ($450–550$ and $1050–1150$: $p = 0.018$, estimated coefficient = $-0.67$; $650–750$ and $1050–1150$: $p = 0.014$, estimated coefficient = $-0.69$).

Functional groups showed different responses to altitude in their abundance (Figure 4, Supplementary information 6). Pond and stream breeders were practically absent from the top two bands, while species with other reproductive habitats were more abundant in the $650–750$ m ($650–750$ and $850–950$: $p = 0.019$, estimated coefficient = $-0.35$; $650–750$ and $1050–1150$: $p = 0.002$, estimated coefficient = $-0.49$), but they did not display any clear linear pattern with altitude. The $< 2.5$ g group was significantly less abundant in the $1050–1150$ m band than at other elevations ($450–550$ and $1050–1150$: $p = 0.001$, estimated coefficient = $-0.79$; $650–750$ and $1050–1150$: $p < 0.001$, estimated coefficient = $-1.15$; $850–950$ and $1050–1150$: $p < 0.001$, estimated coefficient = $-0.88$). The $2.5$ to $10$ g group was most abundant in the $1050–1150$ m band, and the differences between this band and the $850–950$ m one were significant ($p = 0.002$, estimated coefficient = $-0.92$). The $> 10$ g and arboreal groups had a very small number of records, which prevented us from modelling their responses, but...
they were practically absent from the top two bands (Figure 4). Terrestrial species abundance declined with altitude and the lower bands had a significantly higher abundance than the two upper ones. (450–550 and 850–950: p = 0.002, estimated coefficient = −2.25; 450–550 and 1050–1150: p = 0.014, estimated coefficient = −1.15; 650–750 and 850–950: p = 0.006, estimated coefficient = −2.08; 650–750 and 1050–1150: p = 0.04, estimated coefficient = −0.98). For semi-arboreal species the pattern was not clear, but this group was significantly more abundant in the 650–750 band than in the bottom and top ones (450–550 and 650–750: p = 0.046, estimated coefficient = −0.33; 650–750 and 1050–1150: p = 0.015, estimated coefficient = −0.41).

Discussion

Our results show large differences in alpha and beta diversity of the amphibian communities along this altitudinal gradient, as well as differential responses among species dependent on their functional traits. Such changes may indicate communities’ future responses to habitat and climate change. First, alpha diversity declined with increasing altitude. Shannon entropy and Simpson diversity displayed more marked differences between bands than species richness. The two former measures give more weight to dominant species, indicating that the evenness of the community decreased with altitude, in addition to the number of species. This decline in alpha diversity with altitude is the most common trend observed for amphibians [12,13,46–49], but other studies have found increases or multiple peak responses [11,50].

The range of study designs with differences in the groups of amphibians selected, span of the altitudinal gradient studied, scale and surveying methods makes it difficult to pinpoint the reasons behind these differences.

In our study site, the lack of suitable aquatic habitats for reproduction was an important driver of the decrease in alpha diversity with altitude. This is a likely explanation for the absence of pond and stream breeder amphibians in higher altitudes, as bodies of water play an important role in montane areas for amphibian species richness and diversity [10,46]. Areas of higher altitude generally contain fewer ponds due to increased slope, and streams are narrower and carry less water, thus providing fewer adequate breeding habitats for amphibians [13,51]; and this was found to be the case in the upper parts of our study gradient. The predicted important temperature increase expected to occur in the area within the next 25 years [52] would theoretically require species to move several hundred meters upslope to find suitable temperature niches [5]. However, the lack of breeding habitats limits the ability of these species to inhabit upland areas and based on these results we find support for the special vulnerability of lowland species breeding on water bodies to global warming as suggested by Catenazzi [51].

Beta diversity results showed that the upper bands host a very different amphibian community than the lower ones. The range as a whole hosts a diverse and complex amphibian community, including several range-restricted, poorly known species, some of which are potential new species to science or have been only recently described (e.g. Ameerega shihuemoy, Oreobates amarakaeri, Pristimantis spA, Noblella spA).

The higher areas contain a number of species not found at the lower elevations, and thus make an important contribution to the biodiversity and conservation value of the range as a whole. As these high-altitude species are already at the top of the range, they have little margin for upward movements and global warming could force them to migrate up in altitude [5]. This is not possible for these species in this range, and they are likely to face local extinctions if global warming predictions are fulfilled. Protecting the whole altitudinal gradient is important both to preserve maximum levels of biodiversity, due to the high species turnover, and to mitigate the effects of climate change by providing corridors for species migration [7,14,53].

Abundance of the overall community did not show a clear pattern, but there was a decreasing trend with altitude. The relationship between the abundance and density of amphibians and altitude is difficult to discern from the existing literature as the results vary between increases [12,50], decreases [46,47,49] or no clear patterns [13,27], and many studies overlook this dimension altogether [10,11].

While the abundance results for the overall community were difficult to interpret, the patterns for the different functional groups provided more insight. The amphibian communities of these foothill mountains are dominated by small semi-arboreal species of the genus Pristimantis, which reproduce by direct development. However, several functional groups – arboreal, terrestrial, pond and stream breeders, and species over 10 g – are absent or practically absent from the upper areas (with many non-overlapping species between groups). Although the number of individuals in these groups is low overall, the consistent pattern of absence from the upper bands indicates a loss in community complexity and functional diversity with altitude. The lack of aquatic habitats is one likely key to this decrease, but other factors such as prey abundance, productivity and habitat structure may also play a role.

The response of different functional groups to altitude helped to disentangle some of the factors that shape the communities at different altitudes and why these changed along the gradient. However, we suggest that researchers consider the selection and definition of functional traits [20] and the results of
functional groups need to be evaluated carefully. For example, in our study, we used visual encounter surveys which might underrepresent highly arboreal species [35] and this group tends to live in higher parts of the arboreal strata with increasing altitude [54]. Also, our categorization of species in three groups based on maximum adult weight attempts to account for the ecological differences between species but is a subjective classification and could be refined based on the vulnerability of different sized amphibians. Moreover, the link between functional diversity and ecosystem processes is particularly difficult to quantify in the case of amphibians [20], which limits our understanding of the factors that shape these communities and how disruption of the communities might impact ecosystem functioning [55]. Despite these limitations, we strongly recommend considering the functional dimension of diversity in ecological and biodiversity studies, as this can help uncover important patterns that are likely to be overlooked using taxonomic diversity alone. For amphibians, few studies have assessed the changes in functional diversity across environmental gradients, but there are multiple recent studies, besides this one, that show the value of this approach [18,20,56], as well as a database of amphibian functional traits available to support this type of analysis [57].

Conclusions

Altitudinal differences in amphibian communities may be key to understanding ecological patterns and responses to both habitat and climatic change. We show how using several alpha diversity metrics, as well as assessing beta diversity and abundance, helped to demonstrate and better understand these differences. This revealed a decline in diversity with altitude, but no difference in abundance. Furthermore, the high species turnover across the gradient boosted the overall biodiversity and conservation value of the range when considered in its entirety. Splitting the community into functional groups proved very useful for understanding some of the factors likely driving the observed diversity patterns and their potential conservation implications. With this information, we identified two physical factors affecting the diversity and community composition along the range: the presence of water bodies and the height of the range. These two factors suggest an increased vulnerability of certain groups of amphibians to anthropogenic impacts, particularly rapid climate change. These groups include pond and stream breeders, and species restricted to upper elevations. There is much to be gained from the consideration of functional groups in ecosystem biodiversity assessments, particularly for amphibians where there is extensive scope for incorporating a wider selection of functional groups and different altitudinal ranges.

Acknowledgments

Thank you to all the staff members, interns and volunteers of the Manu Learning Centre and The Crees Foundation for their hospitality and help during the research; especially T. Bergan and O. Hill for their help with field work. We thank The Crees Foundation and the Chicago Herpetological Society for logistical and financial support of this research.

Disclosure statement

No potential conflict of interest was reported by the authors.

Geolocation information

Study site: 12°47′21″S; 71°23′28″W (DMS).

ORCID

Jaime Villacampa http://orcid.org/0000-0001-5414-4067
Laura Allen http://orcid.org/0000-0003-0174-9673
Juan E. Malo http://orcid.org/0000-0002-6033-5035

References

[1] Malhi Y, Silman M, Salinas N, et al. Introduction: elevation gradients in the tropics: laboratories for ecosystem ecology and global change research. Glob Change Biol. 2010;16:3171–3175.
[2] Rahbek C. The role of spatial scale and the perception of large-scale species-richness patterns: scale and species-richness patterns. Ecol Lett. 2005;8:224–239.
[3] Chettri B, Bhupathy S, Acharya BK. Distribution pattern of reptiles along an eastern Himalayan elevation gradient, India. Acta Oecologica. 2010;36:16–22.
[4] Sinervo B, Mendez-de-la-Cruz F, Miles DB, et al. Erosion of lizard diversity by climate change and altered thermal niches. Science. 2010;328:894–899.
[5] Raxworthy CJ, Pearson RG, Rabibisoa N, et al. Extinction vulnerability of tropical montane endemism from warming and upslope displacement: a preliminary appraisal for the highest massif in Madagascar. Glob Change Biol. 2008;14:1703–1720.
[6] Laurance WF, Carolina Useche D, Shoo LP, et al. Global warming, elevational ranges and the vulnerability of tropical biota. Biol Conserv. 2011;144:548–557.
[7] La Sorte FA, Jetz W. Projected range contractions of montane biodiversity under global warming. Proc R Soc B Biol Sci. 2010;277:3401–3410.
[8] Sheldon KS, Yang S, Tewksbury JJ. Climate change and community disassembly: impacts of warming on tropical and temperate montane community structure: Climate change and community disassembly. Ecol Lett. 2011;14:1191–1200.
[9] Lawler JJ, Shafer SL, White D, et al. Projected climate-induced faunal change in the Western Hemisphere. Ecology. 2009;90:588–597.
[10] Zancolli G, Steffan-Dewenter I, Rödel M-O. Amphibian diversity on the roof of Africa: unveiling the effects of habitat degradation, altitude and biogeography. Divers Distrib. 2014;20:297–308.
[11] Naniwadekar R, Vasudevan K. Patterns in diversity of anuran along an elevational gradient in the Western Ghats, South India. J Biogeogr. 2007;34:842–853.
[12] Giaretta AA, Facure KG, Sawaya RJ, et al. Diversity and abundance of litter frogs in a Montane Forest of Southeastern Brazil: Seasonal and altitudinal changes.1. Biotropica. 1999;31:669–674.

[13] Phochayavanich R, Voris HK, Khonsue W, et al. Comparison of stream frog assemblages at three elevations in an Evergreen Forest, North-Central Thailand. Zool Stud. 2010;58:632–639.

[14] Garcia-López A, Micó E, Galante E. From lowlands to highlands: searching for elevational patterns of species richness and distribution of scarab beetles in Costa Rica. Divers Distrib. 2012;18:543–553.

[15] Heaney LR. Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and hypotheses. Glob Ecol. 2001;25:15–39.

[16] Harris JBC, Dwi Putra D, Gregory SD, et al. Rapid deforestation threatens mid-elevational endemic birds but climate change is most important at higher elevations. Bradley B, editor. Divers Distrib. 2014;20:773–785.

[17] Lindenmayer D, Blanchard W, Tennant P, et al. Richness is not all: how changes in avian functional diversity reflect major landscape modification caused by pine plantations. Bradley B, editor. Divers Distrib. 2015;21:836–847.

[18] Ernst R, Linsenmair KE, Rödel M-O. Diversity erosion beyond the species level: dramatic loss of functional diversity after selective logging in two tropical amphibian communities. Biol Conserv. 2006;133:143–155.

[19] Sunday JM, Pecl GT, Frusher S, et al. Rapid deforestation threatens mid-elevational endemic birds but climate change is most important at higher elevations. Bradley B, editor. Divers Distrib. 2014;20:773–785.

[20] Riemann JC, Ndriantsoa SH, Rödel M-O, et al. Functional diversity in a fragmented landscape – habitat alterations affect functional trait composition of frog assemblages in Madagascar. Glob Ecol Conserv. 2017;10:173–183.

[21] Lawler JJ, Shafer SL, Bancroft BA, et al. Projected climate impacts for the amphibians of the Western Hemisphere. Conserv Biol. 2010;24:38–50.

[22] Vitt LJ, Caldwell JP. Herpetology: an introductory biology of amphibians and reptiles. USA: Academic Press; 2013.

[23] Ficetola GF. Habitat conservation research for amphibians: methodological improvements and thematic shifts. Biodivers Conserv. 2015;24:1293–1310.

[24] Silvano DL, Segalla MV. Conservation of Brazilian amphibians. Conserv Biol. 2005;19:653–658.

[25] Catenazzi A, von May R. Conservation status of amphibians in Peru. Herpetol Monogr. 2014;28:1–23.

[26] Hof C, Araújo MB, Jetz W, et al. Additive threats from pathogens, climate and land-use change for global amphibian diversity. Nature. 2011;480:516–519.

[27] Catenazzi A, Lehr E, Rodríguez LO, et al. Batrachochytrium dendrobatidis and the collapse of anuran species richness and abundance in the upper Manu National Park, Southeastern Peru: frog declines in the Tropical Andes. Conserv Biol. 2010;2:382–391.

[28] Alan Pounds J, Bustamante MR, Coloma LA, et al. Widespread amphibian extinctions from epidemic disease driven by global warming. Nature. 2006;439:161–167.

[29] Catenazzi A, Lehr E, Vredenburg VT. Thermal physiology, disease, and amphibian declines on the eastern slopes of the Andes: frog declines in the Tropical Andes. Conserv Biol. 2014;28:509–517.

[30] Catenazzi A, Lehr E, von May R. The amphibians and reptiles of Manu National Park and its buffer zone, Amazon basin and eastern slopes of the Andes. Peru Biota Neotropica. 2013;13:269–283.

[31] Whitworth A, Villacampa J Amphibians of the Manu Learning Centre. Chelsea: The Crees Foundation; 2014 [cited 2017 Aug 13]. https://fieldguides.fieldmuseum.org/guides/guide/645.

[32] Villacampa J, Serrano-Rojas J, Whitworth A. Amphibians of the Manu Learning Centre and other areas of the Manu region. Peru: The Crees Foundation; 2017 [cited 2017 Aug 13]. https://www.joomag.com/magazine/fieldguide–amphibians–of–manu/0741739001481300238?short.

[33] Whitworth A, Villacampa J, Serrano Rojas SJ, et al. Methods matter: Different biodiversity survey methodologies identify contrasting biodiversity patterns in a human modified rainforest – a case study with amphibians. Ecol Indic. 2017;72:821–832.

[34] von May R, Donnelly MA. Do trails affect relative abundance estimates of rainforest frogs and lizards? Austral Ecol. 2009;34:613–620.

[35] Doan T. Which methods are most effective for surveying rain forest herpetofauna? J Herpetol. 2003;37:72–81.

[36] Duellman WE. Cusco Amazónico: the lives of amphibians and reptiles in an Amazonian rainforest. USA: Cornell University Press; 2005.

[37] Duellman WE, Lehr E. Terrestrial-breeding frogs (Strabomantidae) in Peru. Germany: Nature und Tier Verlag; 2009.

[38] Beirne C, Whitworth A. Frogs of the Yachana Reserve. UK: Global Vision International; 2011.

[39] R Core Team. R: A language and environment for statistical computing. Austria: Foundation for Statistical Computing; 2018.

[40] Oksanen J, Blanchet FG, Friendly M, et al. Vegan: community ecology package [Internet]. 2018 [cited 2019 Jan 10]. https://CRAN.R-project.org/package=vegan.

[41] Hsieh TC, Ma KH, Chao A. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods Ecol Evol. 2016;7:1451–1456.

[42] Colwell RK, Chao A, Gotelli NJ, et al. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. J Plant Ecol. 2012;5:3–21.

[43] Harrel FE Jr Hmisc: Harrell miscellaneous [Internet]. 2018 [cited 2019 Jan 10]. https://CRAN.R-project.org/package=Hmisc.

[44] Chao A, Chazdon RL, Colwell RK, et al. A new statistical approach for assessing similarity of species composition with incidence and abundance data: a new statistical approach for assessing similarity. Ecol Lett. 2005;8:148–159.

[45] Dray S, Baumman D, Blanchet G, et al. Adespatial: multivariate multiscale spatial analysis [Internet]. 2019 [cited 2019 Mar 3]. https://cran.r-project.org/web/packages/adespatial/index.html.

[46] Ewhan N, Nur Johana J, Shukor MN, et al. Species richness and distributional pattern of amphibians along an elevational gradient at Gunung Raya, Pulau Langkawi, Kedah, Malaysia. Sains Malays. 2018;47:1635–1644.

[47] Fauth JE, Crother BI, Slowinski JB. Elevational patterns of species richness, evenness, and abundance of the costarican leaf-litter herpetofauna. Biotropica. 1989;21:178.

[48] Cortez-Fernandez C. Variación altitudinal de la riqueza y abundancia relativa de los anuros del Parque Nacional y Área Natural de Manejo Integrado Cotapata. Ecol En Boliv. 2006;41:46–64.
Khatiwada JR, Haugaasen T. Anuran species richness and abundance along an elevational gradient in Chitwan, Nepal. Zool Ecol. 2015;25:110–119.

Scott NJ. The abundance and diversity of the herpetofaunas of tropical forest litter. Biotropica. 1976;8:41.

Catenazzi A. Temperature constraint of elevational range of tropical amphibians: Response to Forero-Medina et al.: Letter. Conserv Biol. 2011;25:425.

Marengo JA, Chou SC, Kay G, et al. Development of regional future climate change scenarios in South America using the Eta CPTEC/HadCM3 climate change projections: climatology and regional analyses for the Amazon, São Francisco and the Paraná River basins. Clim Dyn. 2012;38:1829–1848.

Forero-Medina G, Joppa L, Pimm SL. Constraints to species’ elevational range shifts as climate changes: constraints to elevational range shifts. Conserv Biol. 2011;25:163–171.

Scheffers BR, Phillips BL, Laurance WF, et al. Increasing arboreality with altitude: a novel biogeographic dimension. Proc R Soc B Biol Sci. 2013;280:20131581.

Whiles MR, Lips KR, Pringle CM, et al. The effects of amphibian population declines on the structure and function of Neotropical stream ecosystems. Front Ecol Environ. 2006;4:27–34.

Ferreira RB, Beard KH, Crump ML. Breeding guild determines frog distributions in response to edge effects and habitat conversion in the Brazil’s Atlantic Forest. Plos One. 2016;11:e0156781.

Oliveira BF, Sáo-Pedro VA, Santos-Barrera G, et al. AmphiBIO, a global database for amphibian ecological traits. Sci Data. 2017;4:170123.