

Phylogeny, Traits, and Biodiversity of a Neotropical Bat Assemblage: Close Relatives Show Similar Responses to Local Deforestation

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ABSTRACT: If species' evolutionary pasts predetermine their responses to evolutionarily novel stressors, then phylogeny could predict species survival in an increasingly human-dominated world. To understand the role of phylogenetic relatedness in structuring responses to rapid environmental change, we focused on assemblages of Neotropical bats, an ecologically diverse and functionally important group. We examined how taxonomic and phylogenetic diversity shift between tropical forest and farmland. We then explored the importance of evolutionary history by ascertaining whether close relatives share similar responses to environmental change and which species traits might mediate these trends. We analyzed a 5-year data set (5,011 captures) from 18 sites in a countryside landscape in southern Costa Rica using statistical models that account and correct for imperfect detection of species across sites, spatial autocorrelation, and consideration of spatial scale. Taxonomic and phylogenetic diversity decreased with deforestation, and assemblages became more phylogenetically clustered. Species' responses to deforestation were strongly phylogenetically correlated. Body mass and absolute wing loading explained a substantial portion of species variation in species' habitat preferences, likely related to these traits' influence on maneuverability in cluttered forest environments. Our findings highlight the role that evolutionary history plays in determining which species will survive human impacts and the need to consider diversity metrics, evolutionary history, and traits together when making predictions about species persistence for conservation or ecosystem functioning.

Keywords: biodiversity conservation, countryside biogeography, fragmentation, functional traits, occupancy model, phylogenetic diversity.

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Introduction

Human impacts across the globe are intensifying, dramatically altering selective pressures on biological diversity (Barnosky et al. 2012). Yet not all species suffer from the influence of humans; indeed, many use anthropogenic habitats and some even flourish in them (McKinney and Lockwood 1999; Daily et al. 2001; Frishkoff et al. 2014; Mendenhall et al. 2014). Whether the ability to survive and thrive in this modified environment is conserved between close relatives has not been thoroughly explored. Closely related species tend to be phenotypically similar due to the relatively short time-scales since divergence (Hadly et al. 2009). Relatives may also have more similar phenotypes than expected by chance (phylogenetic niche conservatism) either (a) because open niche space tends to be filled by the most ecologically suited extant species, which then can diversify into multiple, closely related, and ecologically similar species, or (b) because strong competition between unrelated lineages in a full community prevents species from leaving their ancestral niches (Losos 2008). If evolutionarily conserved phenotypes determine a species' ability to use a recently emerged novel habitat, we would expect close relatives to exhibit similar responses to deforestation. Understanding how shared traits mediate species tolerance for human-dominated habitats will yield insights into the ecological and evolutionary pressures on species, as well the degree to which complex phenotypes such as deforestation tolerance are phylogenetically conserved and can therefore be predicted from known relationships. This knowledge may additionally inform strategies to slow the losses of biodiversity and the benefits nature provides to society (e.g., Daily 2001; Henle et al. 2004; Meyer and Kalko 2008).

Bat communities can be strongly affected by habitat conversion (Fenton et al. 1992; Medellín et al. 2000). The ma-

majority of bat species are found in the tropics, where deforestation for agriculture is a major cause of biodiversity loss (Ellis et al. 2010; Altringham 2011; Laurance et al. 2014). Bats are both taxonomically diverse, accounting for 20% of mammal species worldwide (Altringham 2011), and ecologically diverse, displaying a wide variety of morphologies, echolocation and foraging styles, diets, and roosting habits. All these traits have been hypothesized to affect species' presence in human-dominated landscapes and sensitivity to human impacts (Meyer et al. 2008; Hanspach et al. 2012).

For most groups of organisms, human-dominated habitats possess fewer species than natural ones—habitat transformation drives loss in taxonomic diversity (e.g., Daily et al. 2001; Mendenhall et al. 2014). But phylogenetic, or evolutionary, diversity is also important, both as an intrinsic property of biodiversity worthy of conservation (Mace et al. 2003) and because it tends to correlate with functional diversity and ecosystem stability (Cadotte et al. 2012; Cadotte 2013). Phylogenetic diversity (PD) may therefore be interpreted as the evolutionary potential of a community to respond to novel impacts (e.g., Cisneros et al. 2015). Yet phylogenetic diversity need not be lost in concert with taxonomic diversity, and relatively few studies have characterized how habitat transformation affects both taxonomic and phylogenetic diversity simultaneously, though there have been recent efforts to investigate these impacts in tree and bird communities (e.g., Arroyo-Rodríguez et al. 2012; Frishkoff et al. 2014; Santos et al. 2014; Edwards et al. 2015), as well as human impacts on coral reef fish communities (D'agata et al. 2014). If human-dominated habitats strongly filter biodiversity based on phylogenetically conserved traits, total PD would decrease faster than expected based on changes in taxonomic diversity alone. Yet conflicting dynamics are reported for bat communities—in some, land-use change appears to boost phylogenetic diversity (e.g., Cisneros et al. 2015), while in others, bat phylogenetic diversity declines with human impact (e.g., Riedinger et al. 2013).

Moreover, despite years of research, how species traits affect the use of human-dominated habitats remains unclear and often varies between landscapes or species (Henle et al. 2004). Bats yield insights into the effect of traits on habitat use because deforestation results in massive simplification of vegetation structure that may affect bat assemblages along dimensions of morphology and flight; echolocation, foraging, and diet; and roosting requirements (e.g., Schnitzler and Kalko 1998; Meyer et al. 2008; Williams-Guillén and Perfecto 2010; Hanspach et al. 2012).

We examine taxonomic and phylogenetic diversity of bats using 5 years of capture data from an agricultural mosaic landscape in southern Costa Rica, using occupancy models that explicitly model and account for variation in species detectability across sites, as well as considerations of spatial scale and spatial autocorrelation. Specifically, we

ask three questions. First, how do species richness and phylogenetic diversity change in human-dominated, agricultural habitats? Second, do evolutionarily close relatives respond similarly to deforestation? Third, which phenotypic traits mediate the response(s) of bats to deforestation? We predict declines in both species richness and phylogenetic diversity in agricultural landscapes compared to forest. We further predict that close relatives will respond similarly to deforestation due to niche conservatism. Specifically, we hypothesize that this will take the form of species possessing morphologies and echolocation strategies adapted for moving through cluttered environments to be more forest restricted, while larger species capable of long-distance travel will be more affiliated with deforested habitats.

Methods

Study Region

We sampled bats in southern Costa Rica in and around the Las Cruces Biological Station (lat. 8°47'N, long. 82°57'W; 1,100 m). The Las Cruces Biological Reserve lies in the Coto Brus Valley and protects roughly 280 ha of primary and mature secondary premontane tropical wet forest (Holdridge 1967). Outside the reserve, the landscape is comprised of pasture, coffee plantations, homes and gardens, and remnant forest fragments (Mendenhall et al. 2014). From the 1500s until the 1960s, the Coto Brus Valley was largely covered in forest, with localized deforestation and maize cultivation prior to initial European contact in Central America (Clement and Horn 2001). Since 1960, the area has been rapidly deforested, with roughly 30%–40% of the land now in pasture, 20% devoted to crop production (primarily, coffee), and 35% covered by remnant forest in mostly 0.1- to 10-ha fragments (Daily et al. 2003; Mendenhall et al. 2011).

Tree Cover

We conducted sampling in 18 sites with varying degrees of local tree cover (fig. 1): three sites were within the only forest reserve in the landscape (tree cover at 50 m: 97.2% ± 1.6%; tree cover at 1 km: 65.8% ± 2.6%); nine sites were located in spatially distinct forest fragments (tree cover at 50 m: 79.9% ± 6.1%; tree cover at 1 km: 41.8% ± 5.3%); and the remaining six sites were in coffee plantations, which typically contain banana plants and scattered trees to create a ~5%–25% canopy cover directly above coffee shrubs (tree cover at 50 m: 17.9% ± 4.3%; tree cover at 1 km: 22.5% ± 1.9%), described in Belisle et al. (2014). Tree cover was calculated at a 2-m resolution by scoring satellite imagery and calculating the area in a given radius covered by any type of tree, whether native or planted (Mendenhall et al. 2011).

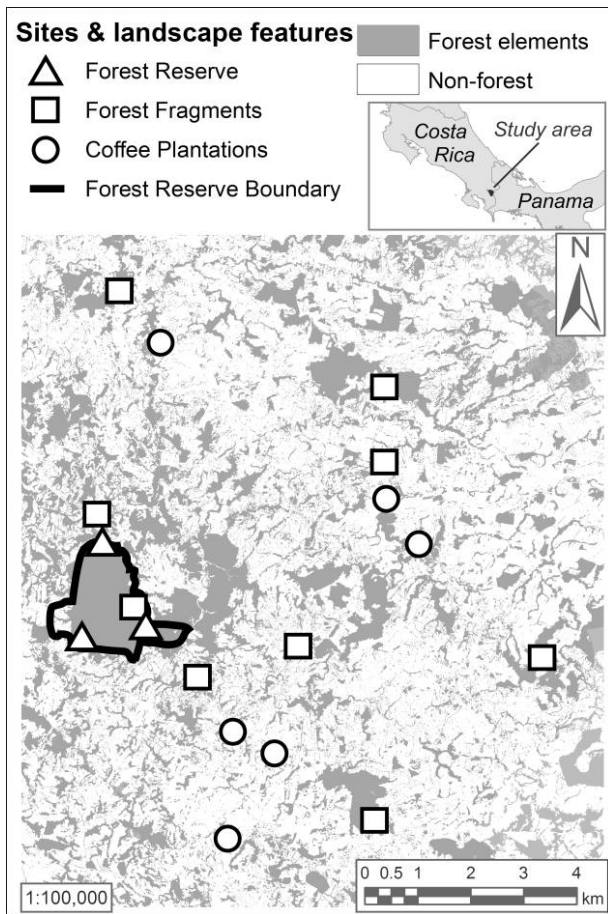


Figure 1: Bats were sampled at 18 study sites across an agricultural landscape in southern Costa Rica. Triangles indicate forest reserve sites; squares indicate forest fragment sites; circles indicate coffee sites. Black outline indicates the border of the Las Cruces Forest Reserve.

Bat Sampling

We sampled bats during the dry season (between Jan. 24 and March 28 in all years) for 4 h each night starting at sunset; each site was sampled on three nights in 2009–2011 and on one night in 2012 and 2013. (Five sites were sampled only once in 2011 due to logistical constraints; see “Supplemental Methods” in appendix, available online.) We chose the dry season as it coincides with the birthing season and is therefore important for population survival, though we acknowledge that bat responses to deforestation may differ in the wet season (e.g., Cisneros et al. 2015).

Bats were captured using a constant-effort mist-netting protocol in which 20 ground-level mist nets (12 m × 2.5 m, 32 mm mesh) were haphazardly distributed in a 3- to 5-ha plot at each site and checked regularly. Captured individuals were weighed and identified (LaVal and Rodríguez-H.

2002; Reid 2009; H. York, R. Timm, B. Rodríguez-H., and R. LaVal, unpublished manuscript).

Phylogenetic Hypothesis

For our phylogenetic hypothesis, we considered two recent phylogenies: a species-level tree of bats (Shi and Rabosky 2015) and a mammalian supertree (Faurby and Svenning 2015). We performed all of our analyses on 100 phylogenies: the maximum likelihood tree, as well as 49 trees randomly chosen from bootstrap replicate phylogenies produced by Shi and Rabosky (2015) and 50 trees randomly chosen from the posterior of trees generated by Faurby and Svenning (2015).

Bat Traits

Body mass was collected from captured bats and averaged to create species means that were used as species-level traits for downstream analyses. Where data from our captures were missing, we used the average mass for the species reported in Reid (2009). We split potential diets into four categories—insectivory, nectarivory, frugivory, and carnivory/sanguivory—and for each species we noted whether each diet category was absent (0), complementary (1), predominant (2), or strict (3), following Rojas et al. (2011) and supplementing their data with data from the literature (tables A1, A2; tables A1–A5 available online). Wing loading, relative wing loading (which removes the influence of mass), and aspect ratio were collected from various literature sources (table A2).

We also examined the peak frequency, bandwidth, and call duration—which impact bat foraging and navigation abilities—of the echolocation calls of each species, taken from Collen (2012). We incorporated roost duration of species as a proxy for roosting requirements. Roost duration is a rough weighted average of the \log_{10} persistence of the roost substrate in days (e.g., leaves that last ~1 week have a roost duration of $1 = 10^1$ days; caves that can last millennia have a roost duration of $6 = 10^6$ days; Patterson et al. 2007). Values for roost duration were either taken from Patterson et al. (2007) or calculated using their formula and data from the literature (table A2).

Phylogenetic Occupancy Model

Failure to acknowledge that detection may vary between habitats or samples can systematically bias results, leading to the incorrect biological inference (Tingley and Beissinger 2013; Iknayan et al. 2014). With bats it is particularly important to consider differences in detectability because survey methods do bias which species are sampled (Kalko 1998), and detectability can vary widely between species and across

habitats (Bader et al. 2015). We used a recently developed variant of the multispecies occupancy model that incorporates phylogenetic information to assess phylogenetic signal in how species respond to environmental gradients (Frishkoff et al. 2017). This phylogenetic occupancy model (POM) estimates the true but unobserved occupancy state (denoted $Z_{i,j,t}$) from underlying occupancy probabilities ($\psi_{i,j,t}$) of all 42 bat species (i) across 18 sites (j) over 5 years (t). The occupancy component estimates species- and year-specific intercepts ($\psi.\alpha_{i,t}$) and species-specific responses to deforestation (denoted $\psi.\beta_i$, where scaled and centered forest cover is Env) with a random effect of species and site ($\psi.\gamma_{ij}$) to account for (potentially spatially autocorrelated) residual differences in species' occupancy between sites. Specifically,

$$\text{logit}(\psi_{i,j,t}) = \psi.\alpha_{i,t} + \psi.\beta_i \times Env_j + \psi.\gamma_{ij}.$$

We incorporated phylogenetic signal in species response to deforestation by assuming that $\psi.\beta_i$ came from a multivariate normal distribution, with covariance structure incorporating phylogenetic information scaled by Pagel's λ parameter (Pagel 1999; Frishkoff et al. 2017). We use the method of de Villemereuil et al. (2012) to integrate phylogenetic uncertainty over 100 possible phylogenies. We checked posterior traces to ensure that mixing across phylogenies was good (ensuring that the Markov chain Monte Carlo [MCMC] did not get stuck on a single phylogeny).

Spatial autocorrelation is commonly present in species occupancy data. To ensure that spatial autocorrelation was directly incorporated in the model and not biasing our other estimates, we directly incorporated it in $\psi.\gamma_{ij}$. Specifically, values of $\psi.\gamma_{ij}$ were drawn from a multivariate normal distribution with covariances defined by distances between sites, modified by an exponential decay term.

The detection component of the model estimated overall detection probability contingent of occupancy ($p_{i,j,t,k}$) using species-specific detection intercepts ($p.0_i$), as well as site-level effects of local terrain ($p.ter$) and vegetation structure ($p.cof$), as these could influence the probability that a bat would be captured. Additionally, an effect of visit number at a site within a year ($p.visit_k$) was included, as bats learn to avoid nets. Specifically,

$$\text{logit}(p_{i,j,t,k}) \sim p.0_i + p.visit_k + p.cof \times Coffee_j + p.ter \times Terrain_j.$$

The relevant spatial scale at which bats respond to landscape heterogeneity is unknown. Accordingly, we incorporated scale selection directly into the model by considering spatial scale to be a free parameter that determined variable Env (Frishkoff et al. 2017b). In this way, the model searched for the radius at which the proportion of tree cover best explained the bat detection data and ignored spatial scales that did not explain the data. This yielded a posterior

distribution of reasonable spatial scales that affect bats. After running the initial model on the data without the traits, we used the posterior-modal spatial scale in the trait models. For trait models, we allowed total $\psi.\beta_i$ to be made up of an across-species mean response, an effect of the focal trait, and (phylogenetically conserved) species' specific residual variation. The full description of model structure is available in the appendix.

POMs were implemented using the JAGS language with the R package R2jags (Su and Yajima 2014). JAGS provides a Bayesian framework for parameter estimation. In all cases, we used vague priors. We ran all models with three chains for 30,000 iterations, a thinning interval of 30, and 15,000 iterations discarded as burn-in, resulting in 1,500 samples of the posterior. We checked convergence by visually inspecting trace plots and through the Gelman-Rubin convergence diagnostic (Gelman and Rubin 1992), ensuring that all values were less than 1.1. The convergence diagnostic is a summary statistic that measures variance between and across multiple MCMC chains; it reaches 1 when each chain's variance is equivalent to the total variance of all chains, indicating that the MCMC has converged onto a well-defined region of parameter space.

Calculating Species Richness and Phylogenetic Diversity from Occupancy Models

To account for imperfect detection in species richness and phylogenetic diversity (PD; Faith 1992) and phylogenetic species variability (PSV; Helmus et al. 2007) and clustering (mean phylogenetic distance [MPD] Z -score), we calculated these metrics from the posterior draws of the occupancy model's MCMC algorithm. Each iteration of the MCMC generated a plausible occupancy state for all species in all sites over all years of the study ($Z_{i,j,t}$). Species richness was simply calculated as the sum of species at a site in a year within the posterior occupancy state array. Similarly, PD, PSV, and MPD Z -scores were calculated over each iteration of the MCMC, yielding posterior distributions for phylogenetic diversity in each site-by-year combination. To calculate an MPD Z -score, data must be compared to a null model. We used the trial-swap algorithm instituted within *picante* (Kembel et al. 2010) to maintain both row and column sums of the site-by-species matrix for each iteration along the MCMC. We used 999 permutations to derive null distributions from which to calculate Z -scores.

To examine the effects of tree cover on these community metrics, posterior means were regressed against tree cover using a generalized linear mixed-effect model, with a random intercept of year, and a site effect incorporating spatial exponential decay of correlation as a function of distance between sites (to account for potential spatial autocorrelation). Linear and quadratic effects of tree cover were tested.

Significance was determined with likelihood ratio tests, evaluated against a χ^2 distribution.

Testing Traits

We tested whether morphological characteristics, echolocation characteristics, primary dietary guild, and roost preferences might predispose different bat species to affiliate more strongly with forest or agriculture. To do so, we reran phylogenetic occupancy models but used trait information as a linear predictor of species response to deforestation ($\psi.\beta_i$), allowing us to explore the interaction of trait and environment while controlling for phylogenetic nonindependence. We also tested for phylogenetic signal in each of the traits. See appendix for details on trait-based POMs. Capture and site data, R code, and JAGS code underlying the models are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.mb552> (Frank et al. 2017).¹

Results

We recorded 5,011 total bat captures across the 180,480 mist net meter hours. We detected 42 species: 36 species in forest reserves, 36 species in forest fragments, and 31 species in coffee plantations. Species varied in their detection probability, and detection probability of all bats declined within a year as sites were revisited—indicative of trap aversion in these species (Marques et al. 2013). Neither a site's primary land cover (forest or coffee) nor the general terrain around the site (e.g., hilltop or valley) affected detection probabilities after accounting for species-specific effects (table A3). Bat occupancy was significantly spatially autocorrelated, and this correlation decayed at a rate such that it was reduced by half over a distance of 4.0 km (95% Bayesian credible interval [BCI]: 2.2 km, 9.0 km; fig. A1; figs. A1–A6 are available online). After accounting for this spatial autocorrelation, species' response to tree cover was best described by the proportion of tree cover within a 50-m radius of the capture site (95% BCI: 20 m, 110 m; fig. A2).

After accounting for spatial autocorrelation, both detection-corrected bat species richness and total phylogenetic diversity varied linearly with local tree cover, with the greatest diversity in forest reserve sites and the least in agriculture (species richness linear tree cover term, $df = 1$, $\chi^2 = 55.6$, $p < .001$; PD linear tree cover term, $df = 1$, $\chi^2 = 131.2$, $p < .001$; fig. 2). PSV also declined in agriculture but demonstrated accelerating loss of evolutionary history and phylogenetic clustering as tree cover diminished (quadratic tree cover term, $df = 1$, $\chi^2 = 9.6$, $p = .002$; fig. 2). Patterns of the net relatedness index showed concordant patterns, with

agricultural communities being slightly phylogenetically clustered and forest communities being slightly overdispersed (fig. A3).

These assemblage-wide patterns emerge as the result of individual species' responses to land-use change. Overall, most species tended to increase their occupancy probability with increasing tree cover (mean logit-scale response = 1.83, 95% BCI: -0.28 , 4.38), though there was large inter-specific variation (fig. 3). For 27 species, the mean posterior habitat affiliation coefficients ($\psi.\beta_i$) indicated increasing occupancy probability with greater tree cover (mean posterior of $\psi.\beta_i$ greater than zero), while 15 species decreased in occupancy (mean posterior of $\psi.\beta_i$ less than zero). Of the 42 species, 8 could be classified as clearly forest affiliated with certainty (95% BCI was entirely above 0), while only 4 were firmly deforestation affiliated (95% BCI was entirely below 0). The most strongly forest-affiliated species included three species of *Micronycteris* and three species of *Myotis*. *Phyllostomus hastatus*, *Sturnira parvidens*, *Lonchophylla robusta*, and *Uroderma bilobatum* affiliated strongly with deforested coffee plantations.

At the species level, we found phylogenetic signal in the response of bats to tree cover (posterior mode of $\lambda = 0.68$, 95% highest posterior density: 0.16, 1.0; fig. A4). Additionally, close relatives were more similar to one another than expected by chance in all tested traits (table A4). Yet, of these, only body mass and absolute wing loading strongly contributed to determining whether a species was forest or agriculture affiliated. Absolute wing loading and body mass, however, were highly correlated with one another ($\rho = 0.86$). When both traits were considered together, the contribution of absolute wing loading alone explained as much variation as including both mass and wing loading (proportion of total habitat affiliation explained by traits from both models = 0.48). Both larger bats and those with higher wing loadings tended to be associated with agriculture (fig. 4; table A5). As a result, bat assemblages in deforested sites had larger mean body size than those of forest sites (fig. A5; likelihood ratio = 47.4, $p < .001$). This trend was primarily driven by the strong affiliation of a number of small-bodied bats (i.e., *Micronycteris* spp.) with forest and the occurrence of the two largest species (*Vampyrum spectrum*, the largest Neotropical bat species, and *Phyllostomus hastatus*) in two agricultural sites. Wing aspect ratio, relative wing loading, echolocation call parameters, roost duration, and all diet categories were not predictive of a bat's habitat usage.

Discussion

Declines in Taxonomic and Phylogenetic Diversity with Deforestation

At the assemblage level, we observed declines in species richness, phylogenetic diversity, and PSV in deforested areas.

1. Code that appears in *The American Naturalist* is provided as a convenience to the readers. It has not necessarily been tested as part of the peer review.

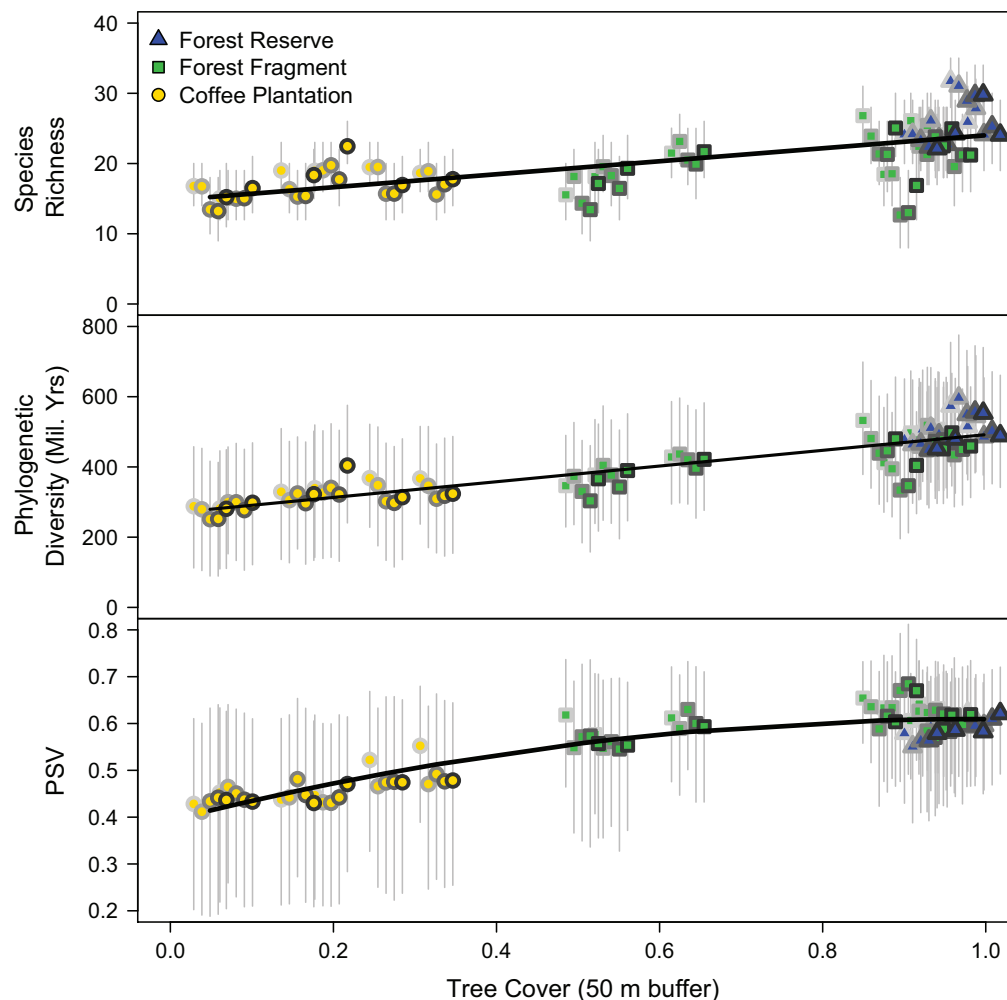


Figure 2: Detection-corrected species richness, phylogenetic diversity, and phylogenetic species variability (PSV) increase with tree cover. Shapes show each year of data, with years staggered along the X-axis for visibility (2009 bordered in white at left, 2013 bordered in black at right). Thin lines depict 95% Bayesian credible interval for each point's estimate. Best-fit lines represent post hoc maximum likelihood linear regressions based on each year's posterior mean for each site, with a fixed effect of tree cover and random effects of site and year.

Interestingly, PSV declines even more sharply than species richness does, suggesting that some clades are more sensitive to deforestation than others. These losses in PSV were accelerating—indicating that incremental increases in tree cover in agricultural environments could have disproportionately beneficial outcomes for phylogenetic diversity, above and beyond mere increases in species diversity. This pattern of phylogenetic clustering in agricultural sites (fig. 2) complements our finding of phylogenetic signal in the responses of close relatives to deforestation (fig. 3), demonstrating how assemblage-wide patterns derive from the responses of individual species. In our case, we observe that most of the species prefer forest but nonetheless use agriculture to some degree. Non-phylostomid species and some phylostomid genera (e.g.,

Miconycteris) tend to be strongly forest affiliated in our data set. Agriculture-affiliated species tend to be distributed throughout the phyllostomid clade. The finding that some clades and species have habitat affiliations that diverge from their close relatives emphasizes the utility of considering both assemblage-level and species-level analyses when making inferences about human impacts on species and communities for conservation considerations.

Declines in Taxonomic and Phylogenetic Diversity at Local versus Landscape Scales

Previous examinations of bats at coarser spatial scales in human-altered landscapes have shown similar declines in

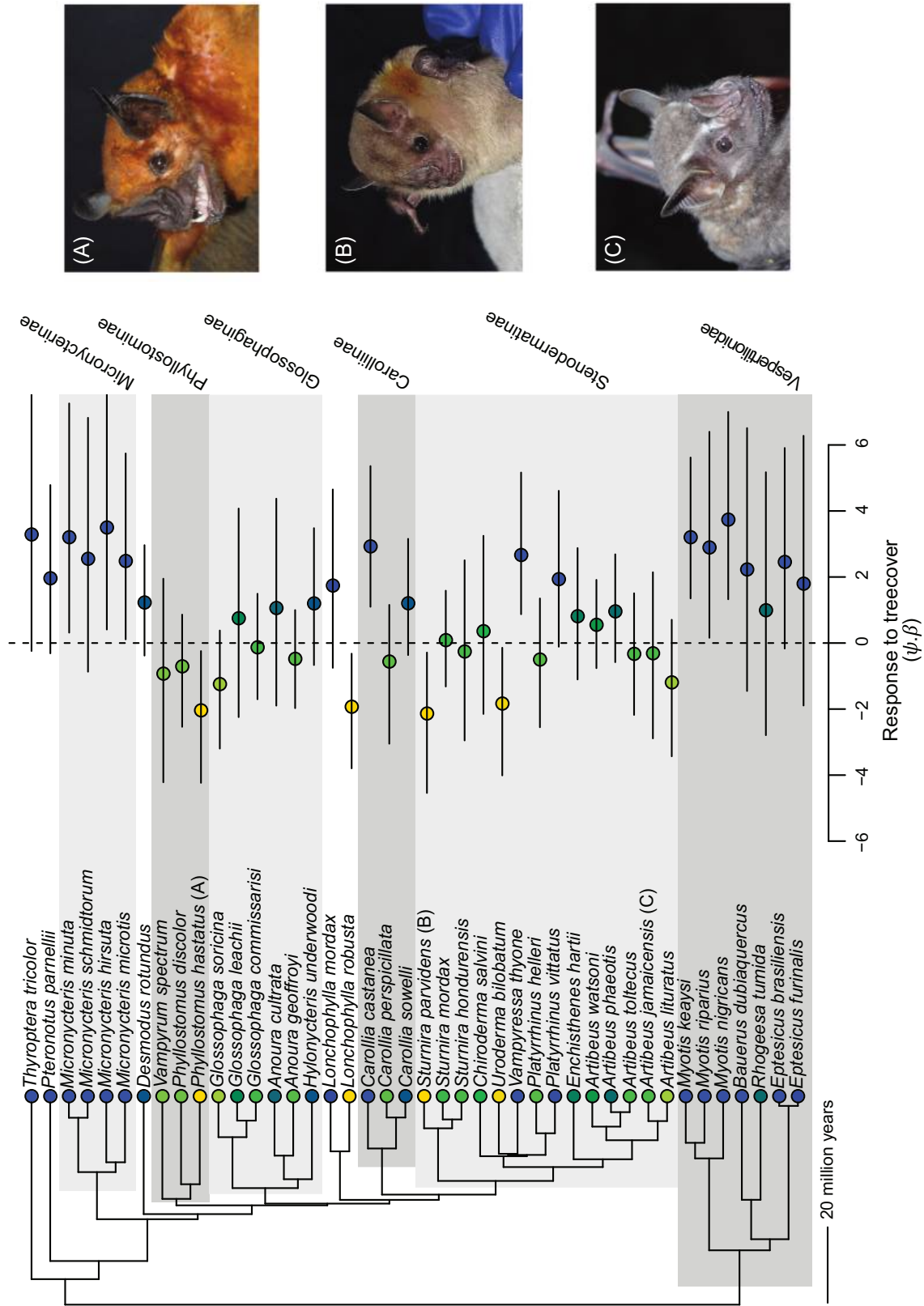


Figure 3: Responses to deforestation show phylogenetic signal in bats. Tip colors on the bat phylogeny (left) correspond to each species' habitat affiliation, as determined through the complete occupancy model; scale bar represents 20 million years. Circles (right) represent the posterior means of the estimated coefficients; lines represent 95% Bayesian credible intervals. Letters following phylogeny correspond to the pictured bat species. Bat families or phyllostomid subfamilies containing more than two species are indicated by shaded boxes and labeled; phyllostomid subfamilies are labeled according to Baker et al. (2003). Photo credit: Jon Flanders.

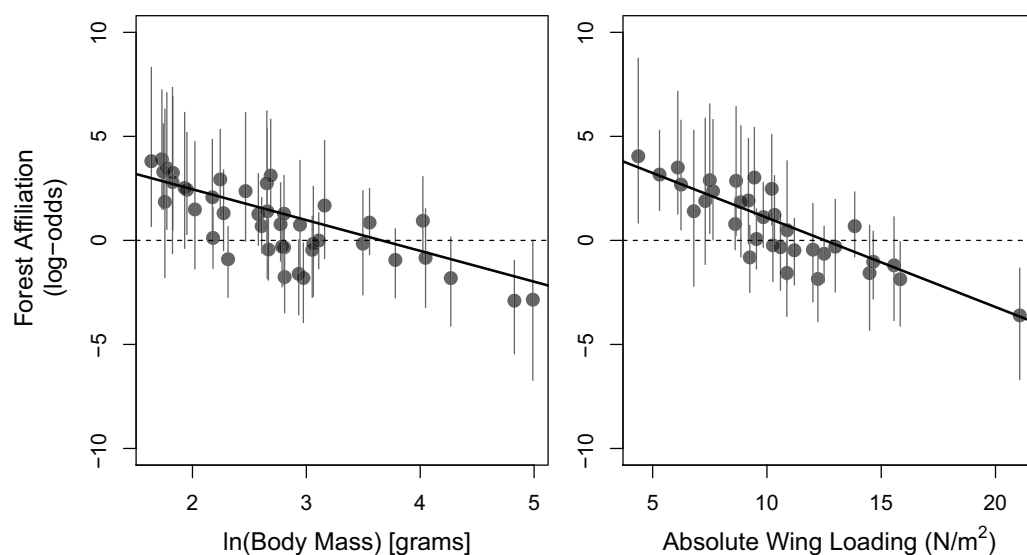


Figure 4: Large species with high wing loading are more likely to occupy deforested habitats. Circles represent individual species, with placement along the Y-axis representing occupancy model-inferred affiliation with forest habitat ($\psi.\beta$ parameter; representing the log odds that the species will occupy a forest vs. an agricultural habitat). Lines indicate 95% Bayesian credible interval of forest affiliation, and the best-fit line indicates the occupancy model's estimate of the posterior mean of the relationship between the trait of interest and forest affiliation ($\psi.\beta$). Wing loading is in units of Newtons per meter squared.

phylogenetic and taxonomic diversity. Riedinger et al. (2013) found greater phylogenetic clustering (MPD Z -score) in Bavarian regions with greater urban land cover, though they found no impact of farmland on bat species richness or overall phylogenetic diversity. Cisneros et al. (2015) focused on landscape effects on bat communities, while holding habitat status constant in a lowland Costa Rican bat assemblage. These surveys in forest patches of varying size and surrounded by different land uses (examined at 1- to 5-km spatial scales) during the dry season found that taxonomic (Simpson's diversity index) and phylogenetic (Rao's Q) diversity increased with greater proportions of pasture in the region. While this is the opposite pattern that we observe, the landscape contexts and scales of our two studies are quite different. In their case, they concluded that environmental heterogeneity (i.e., areas with forest and pasture) provides diverse sets of resources to support correspondingly diverse sets of bat species (Cisneros et al. 2015). Thus, landscapes with both agriculture and forest may maximize diversity (because of community complementarity) even while deforestation at the local scale denudes alpha diversity through habitat filters and may result in some landscape-wide extinctions.

It may be surprising that bats seem to be reacting on such a local scale, given their mobility (many traveling 0.5–2.5 km per night or more [Bernard and Fenton 2003]). Indeed, bat habitat metrics are often examined on scales of between 1 km and 5 km (e.g., Gorresen and Willig 2004;

Cisneros et al. 2015; Farneda et al. 2015). However, there is ample evidence from bat communities globally that local scale factors (100–400 m) can strongly impact bat community and individual species responses (e.g., Fahr and Kalko 2011; Bellamy et al. 2013; Wordley et al. 2015; Chambers et al. 2016). Because of the fine-scale nature of both our community and environmental data, we were able to show that bat communities respond to habitat conversion at extremely small spatial scales, on the order of 50 m. By incorporating considerations of fine spatial scale into investigations of phylogenetic diversity, we show that declines in the evolutionary history of surviving lineages may occur even when the landscape as a whole contains suitable habitat. Certainly, bat persistence relies on the greater landscape context, but future studies should consider investigation of small-scale impacts as well, if they have the spatial resolution, since both are likely important (e.g., Chambers et al. 2016). Population survival will depend on organismal level responses, and landscape-level patterns of occurrence or exclusion ultimately emerge as the result of incremental increases in usable habitat at local scales. This may be particularly important when considering diversified agriculture in rural, tropical landscapes where human-altered land uses are integrated with remnant natural habitats. Much of the Earth's biodiversity remains in these mosaic landscapes, rather than highly intensive and extensive agricultural systems, as is the case in many agroecosystems, for example, Europe or the United States.

While we expect our core findings (loss of taxonomic and phylogenetic diversity, presence of phylogenetic signal in response to habitat conversion, and wing loading as a key trait predicting habitat affiliation) to be generalizable across bat communities in multiple landscape types, this clearly remains an open question. Ultimately, generalizability to other landscapes, with more intensive and extensive forms of agriculture is dependent on the degree to which the landscape scale acts to filter the regional species pool, independent of the local scale habitat filters examined here. In the future, the relative power of these scales may be effectively addressed through hierarchical models that split landscape-level processes (that filter the regional species pool into multiple landscape pools) from local-scale processes (that filter species from a site's landscape species pool into individual habitat patches).

Concordance with Other Taxa

The reduction of phylogenetic diversity of bat assemblages in agricultural areas uncovered in this study supports findings from other taxa. In a large, multiyear study of birds in Costa Rica, bird species richness was similar in forest and more wildlife-friendly forms of agriculture, but phylogenetic diversity declined steeply in agriculture (the result of phylogenetic clustering), with half of the variation in species-specific affiliation with agriculture explained by Brownian motion evolution through the phylogeny (Frishkoff et al. 2014). Similarly, bird phylogenetic diversity in Colombia was lower in cattle pastures than forests; forests supported more evolutionarily distinct lineages, but certain clades thrived in farmed habitat (Edwards et al. 2015). Phylogenetic diversity of trees and other plants also declines in deforested, fragmented, and urbanized areas, though these patterns vary (e.g., Knapp et al. 2008; Santos et al. 2010, 2014; Arroyo-Rodríguez et al. 2012). Similarly diverse threats related to human activity are predicted to reduce mammalian phylogenetic diversity globally (Jono and Pavoine 2012). Though the impacts of agriculture and deforestation on phylogenetic diversity broadly are still uncertain, mounting evidence suggests that habitat conversion selects for specific clades and lineages while causing the decline of community-wide phylogenetic diversity.

Some Traits Explain Trends in Deforestation Tolerance

In birds, bats, and trees, it appears that some aspect of the human-altered environment is favoring only a subset of the total biological diversity found in tropical forests, consistent with a response in which lineages are filtered based on shared traits. This pattern is expected from environmental perturbations generally, for example, in disturbed lake

environments (Helmus et al. 2010). In our data set, absolute wing loading (which is strongly correlated with mass) was the strongest predictor of habitat affiliation. This finding is consistent with studies that have observed that larger bats with higher wing loadings are more tolerant of human-dominated habitats—presumably because they are able to traverse open habitats more efficiently than smaller bats (e.g., Hanspach et al. 2012; Marinello and Bernard 2014). It does, however, contrast with other studies in which large bats were more vulnerable to forest fragmentation (e.g., Farneda et al. 2015). Similarly, large birds have been found to be more mobile and affiliated with habitats near agriculture (e.g., Neuschulz et al. 2013), though some large-bodied species may be less able to survive in deforested areas (e.g., Cleary et al. 2007).

While bat size and maneuverability (represented by absolute wing loading) are important predictors of habitat affiliation, roughly half of the variation in habitat affinity is likely due to species-specific or landscape-specific factors. For example, the genus *Carollia* makes up 58% of captures at a recovering pasture site within the forest reserve but only between 10% and 30% of the captures in forest reserve sites with similar surrounding tree cover. Because *Carollia* spp. often feed on the fruits of secondary-growth plants (Reid 2009), which are presumably more abundant in this gap environment than in closed forest, we can speculate that it is the presence of specific food resources and not the tree cover per se that is determining the bat assemblage at this site. Additionally, bat communities are known to respond to multiple landscape features involving configuration and structure that were not measured here, which if correlated with local tree cover, may affect the habitat affiliations we inferred (e.g., Cisneros et al. 2015; Farneda et al. 2015). Other types of species-level traits may also explain habitat affiliation; for example, in mammals, species with larger brains were better able to survive in novel, predominantly human-generated environments (Sol et al. 2008).

Finally, habitat affiliation may also depend on a variety of underlying traits that manifest themselves differently depending on environmental conditions. For example, in amphibians, thermal tolerance governs tolerance to deforestation, but the forest affiliation of a particular population depends on elevation, because both forests and deforested agricultural sites become colder at higher altitudes (Frishkoff et al. 2015; Nowakowski et al. 2017). As a result, the same frog species can be strongly forest affiliated in the lowlands but strongly agriculture affiliated upslope (Frishkoff et al. 2015). Capacity for such habitat switching along biogeographic gradients has also been observed in tropical birds and beetles (Larsen 2012; Frishkoff et al. 2016). Therefore, although many of the species we examined are widely distributed throughout the Neotropics and exhibit many of the morphologies, diets, and habits of bats more generally,

it is entirely possible that these same species might show a different response to deforestation in different regions.

The Benefit of Detailed, Small-Scale Studies of Diversity-Disturbance Relationships

By considering many factors that are common, and often unavoidable, in ecological studies (e.g., spatial autocorrelation, spatial scale considerations, biases in detection, species-specific responses), we were able to uncover changes in the evolutionary history preserved across the landscape, as well as the susceptibility of individual clades to deforestation. Detection probability is not constant across species, and failure to take this into account can bias results, especially in community-wide metrics such as species richness or PSV (Tingley et al. 2012). In our case, accounting for imperfect detection both increased the number of species inferred to be present in each site and increased the effect of deforestation in biodiversity declines, highlighting the importance of incorporating detection probability into studies of biodiversity change (see fig. A6; cf. fig. 2). Additionally, by incorporating spatial autocorrelation and integrating spatial scale selection directly into the model, we were able to detect local-scale patterns that would have been missed had we tested at only broad spatial scales based on a priori decisions due to the high mobility of bats. Only by examining species richness, phylogenetic diversity, phylogenetic signal among close relatives, and trait-based occupancy patterns through a detection and spatially corrected framework were we able to hone in on the determinants of lineage persistence in natural environments, identifying individual species responses and trait-based determinants of habitat affinity.

The methods we used to consider multiple confounding ecological factors and the suite of approaches to them can be applied to any system to improve estimates of biodiversity change across gradients but require copious, detailed data; in our case, the fine-scale resolution of our data (tree cover at 2-m resolution) allowed us to investigate spatial scales that are often unattainable with remote sensing data. Acquiring such data is expensive and time consuming and, therefore, likely beyond the scope of most studies, yet such in-depth studies can yield important insights to complement broader-scale studies and meta-analyses, generating mechanistic hypotheses for large-scale patterns.

Conclusions

We sought to determine whether phylogenetically conserved phenotypes could predict the responses of lineages to evolutionarily novel habitats and explain assemblage-level patterns by investigating patterns of diversity change, similarity of responses to deforestation between close relatives, and the predictive ability of traits. We observed biodiversity de-

clines, both taxonomic and phylogenetic, with loss of local tree cover. Loss of phylogenetic diversity outpaced loss of species richness, because closely related species shared similar responses to deforestation, leading entire clades to vanish from agricultural environments, while no particular clades preferred agriculture. The species least suited to agricultural habitats were small species with low wing loadings, more adept at navigating enclosed spaces.

Examinations of phylogenetic diversity changes in altered landscapes and inquiries into the mechanisms driving these changes are still relatively rare. It remains to be seen whether other taxa experience accelerating losses of phylogenetic diversity with deforestation and whether these declines hold across other regions of the world. The finding that phylogenetic diversity of highly mobile organisms is sensitive to local-scale deforestation suggests that conservation decisions must consider organisms' immediate environments as well as coarse landscape-level features. Consideration of both assemblage-level metrics and individual species' responses will help researchers and conservationists alike as they try to formulate predictions about the impact of humans on wild populations.

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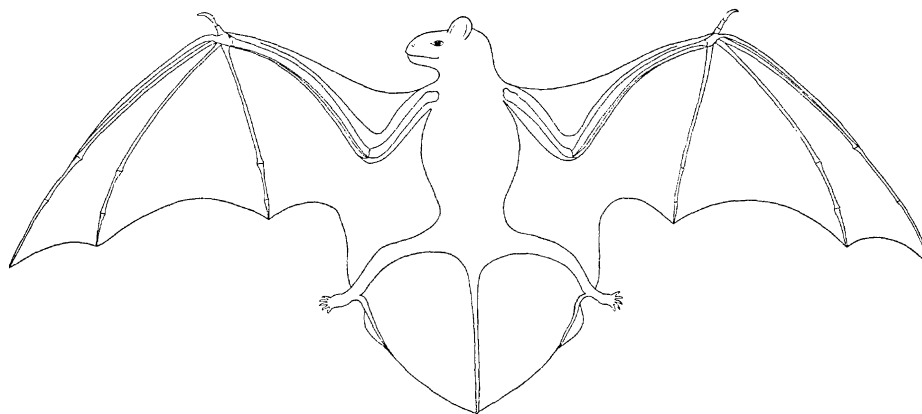
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