



# The role of frugivory in the diversification of bats in the Neotropics

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## ABSTRACT

**Aim** Ecological interactions are among the most important biotic factors influencing the processes of speciation and extinction. Our aim was to test whether diversification rates of New World Noctilionoidea bats are associated with specialization for frugivory, and how this pattern differs between the mainland and the West Indies.

**Location** The New World.

**Methods** We reconstructed a time-calibrated molecular phylogenetic hypothesis for the New World genera of the superfamily Noctilionoidea. We compiled data on diet, morphology, geographical distribution and number of ecoregions in which each genus occurs. Then, using the phylogenetic tree constructed, we tested whether diversification was driven by diet (animalivorous and sanguivorous versus nectarivorous and frugivorous) and specialization for frugivory. Afterwards, we conducted phylogenetic comparative analyses to identify correlates of species richness and net diversification rates.

**Results** The diversification rate was higher in mutualistic than in antagonistic clades in mainland and Antillean biogeographical scenarios, but only strictly frugivorous clades showed a markedly higher diversification rate than the rest of the genera. Geographical range and number of ecoregions were positively associated with species richness and diversification rate in continental and insular lineages. Lower body mass, lower forearm length and specialization for frugivory were significantly positively correlated with higher diversification rates in continental lineages, whereas these parameters were negatively correlated in Antillean lineages.

**Main conclusions** The direction of the relationship of intrinsic factors (specialization for frugivory and body size) with diversification of noctilionoid bats depends on the biogeographical context, whereas the direction of the relationship of extrinsic factors (geographical range and number of ecoregions) with diversification is consistent in both mainland and the West Indian lineages.

## Keywords

Antilles, diversification, extinction, frugivorous bats, mutualism, Noctilionoidea, Phyllostomidae, speciation, timetree.

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## INTRODUCTION

The latitudinal diversity gradient (i.e. species richness decreases from tropical to extratropical areas) and the difference in species richness between islands and the mainland (i.e. generally islands have fewer species per unit area than the

mainland) are two spatial patterns that have interested biogeographers for decades. The diversification rate hypothesis is one of the evolutionary explanations for the latitudinal variation in biological diversity that has received greatest support (Mittelbach *et al.*, 2007). According to this hypothesis, there are higher rates of speciation and lower rates of

extinction in the tropics. The time-for-speciation effect, which holds that tropical climates are older and historically larger, thus allowing more opportunities for diversification, also explains many latitudinal and elevational diversity patterns (Wiens, 2011). Tropical niche conservatism (Wiens & Donoghue, 2004) is another historical mechanism that may explain the latitudinal diversity gradient, although the effects of this hypothesis are hard to distinguish from the time-for-speciation effect, and both mechanisms may simultaneously contribute to the distributional patterns (Stevens, 2011).

Area, isolation, habitat diversity, availability of empty niches and *in situ* speciation rate are island characteristics that explain the pattern of differences in island–mainland species richness (Algar & Losos, 2011). In oceanic islands, colonization and extinction events may explain species richness in small islands, while cladogenesis may explain species richness in islands of larger size (Losos & Schluter, 2000). The effect of *in situ* speciation on island–mainland richness difference could be related to whether islands can support fewer species than similarly sized mainland regions or to whether diversification rates are greater in islands than within the mainland, among other factors (Algar & Losos, 2011).

Furthermore, comparative studies in plants and vertebrates indicate that variation in species richness among clades depends on extrinsic factors (e.g. climatic conditions, vegetation types, habitat structure and the variety, and abundance of resources), which provide the ‘opportunity for diversification’ (Gonzalez-Voyer *et al.*, 2011). Phylogenetic patterns of species richness also depend on intrinsic species characteristics (e.g. body size, vagility, and dietary specialization), which may constitute key innovations that shape the process of diversification (Gonzalez-Voyer *et al.*, 2011).

Thus, ecological factors (e.g. physiological tolerances, biotic interactions), evolutionary factors (e.g. parapatric and sympatric speciation, genetic drift and rate of diversification) and biogeographical factors (e.g. geographical distribution of populations, climatic variation, and area) should be considered to explain richness patterns. However, the ultimate explanation lies in the three processes that directly modify the number of species in a given location: speciation, extinction and dispersal (MacArthur & Wilson, 1967; Ricklefs, 1987). Considering this, patterns of species richness are best understood by determining the ecological, evolutionary and biogeographical correlates of clade richness and diversification, and establishing how the variation in speciation and extinction rates drives those patterns (Wiens, 2011).

Ecological interactions are among the factors influencing the processes of speciation and extinction (Thompson, 1994; Schluter, 2000). Interspecific competition, for example, was determined experimentally to be the main interaction driving divergent selection (Schluter, 2000; Rundle & Nosil, 2005). Predation has been also demonstrated experimentally to drive phenotypic divergence, and therefore has an important role in driving adaptive radiations (Meyer & Kassen, 2007).

The role of mutualistic interactions is less clear. For instance, mutualistic interactions in which phenotype match-

ing occurs (e.g. obligate pollinator mutualism) restrict diversification (Yoder & Nuismer, 2010). Selection generated by pollinator shifts promotes morphological diversification but does not promote species diversity (Whittall & Hodges, 2007). The divergent use of the same pollinator by some plant genera is considered to be a mode of pollinator-driven diversification (Johnson, 2010) but is better explained by competition leading to character displacement (Armbruster & Muchhala, 2009). On the contrary, van der Niet & Johnson (2009) found floral but not vegetative divergence in many sister species from five plant orders, which suggests that pollinators are of importance in the diversification of plants.

The role of frugivory in the diversification of mutualists, and particularly in the diversification of frugivores, has received less attention (but see Gómez & Verdú, 2012). Evidence of reciprocal specialization between plants and frugivores is scarce in comparison with data for pollination systems. Therefore a suitable system for conducting studies of phenotypic diversification that may lead to species diversification among frugivores is harder to find. Yet, a statement about frugivory underlies the evolutionary studies of the greatest adaptive radiation in a mammalian family, the leaf-nosed bats of the family Phyllostomidae (Freeman, 2000). This New World family is the most taxonomically diverse among bats in terms of number of genera, and it comprises the highest number of feeding strategies within the order Chiroptera (Simmons, 2005). Frugivory has been proposed as the ecological interaction that allowed morphological and ecological diversification of the family (see the revision in Rojas *et al.*, 2011). The current species diversity pattern of Phyllostomidae and of Pteropodidae, the other bat family in which frugivory evolved, could be a reliable indicator of the evolutionary success of the shift from insectivory to frugivory. These two families account for almost a third of the number of extant species of bats (Simmons, 2005). Furthermore, the overlap in increased diversification between flowering plants and phyllostomids during the Eocene and Oligocene (Jones *et al.*, 2005) may suggest a positive correlation in the diversification of flowering and fleshy-fruit-producing plants with their mutualistic chiropteran counterparts.

A recent phylogenetic comparative analysis of ecomorphological associations of diet with mandible shape suggests that speciation in the first 10 million years of phyllostomid evolution was probably the result of dietary shifts, among other factors (Monteiro & Nogueira, 2011). In another recent study, Dumont *et al.* (2012) reported that the emergence of a new skull shape in stenodermatine bats was evolutionarily related to increases in speciation rate and trophic evolution. This trophic evolution consisted of an increase in the proportion of fruit in the diet. The authors proposed that biting performance linked to the morphological innovation unlocked ecological opportunities for phyllostomid bats to diversify. The results support the hypothesis that frugivory might play a key role in the diversification of mutualists. Other sources of ecological opportunities (e.g. occupation of new

habitats; Yoder *et al.*, 2010) that could favour the diversification of phyllostomid bats remain to be explored.

The family Phyllostomidae is a good study system for testing whether frugivory promotes diversification. Fruit consumption is present to a greater or lesser extent across this family, with the exception of a few monotypic or poorly diversified genera (Rojas *et al.*, 2011). The gradient from non-frugivorous genera (i.e. animalivorous and sanguinivorous) to strictly frugivorous genera comprises all feeding habits in the family. Species with a mixed habit or those that feed mainly on nectar and pollen can be classified as complementary or predominantly frugivorous. In addition, this family co-occurs with the other New World families of the superfamily Noctilionoidea (Teeling *et al.*, 2005), which are represented by animalivorous lineages. These five families (Thyropteridae, Furipteridae, Noctilionidae, Phyllostomidae, and Mormoopidae) constitute a monophyletic clade (Meredith *et al.*, 2011), and at a smaller spatial scale usually co-occur in mainland Neotropical and Antillean assemblages (e.g. Kalko *et al.*, 1996; Rodríguez-Durán & Kunz, 2001). We are of the opinion that a better approach for assessing the role of frugivory in the diversification of phyllostomids should include both the evolutionary (superfamily Noctilionoidea) and geographical (mainland and islands) frameworks in which the family diversified.

We predict a different relationship between specialization for frugivory and diversification in islands and the mainland. Insular biotas are usually species-poor and disharmonic, and island endemics tend to have reduced dispersal ability, higher population densities, a decrease in fecundity, larger or smaller body sizes, broader ecological niches and elevated rates of extinction compared with their continental relatives (Whittaker & Fernández-Palacios, 2007). Species impoverishment in islands, for example, might cause variations in ecological generalization in both mutualistic animals and plants (Olesen & Jordano, 2002). These super-generalists may shape the evolutionary dynamics of the mutualistic networks by increasing trait complementarity (i.e. a high degree of trait matching between mutualistic partners) and trait convergence (i.e. trait similarity that emerges as a response to similar selective pressures) (Guimarães *et al.*, 2011). Alternatively, specialization could compromise diversification of insular strict frugivores because such lineages have a reduced niche breadth in comparison with the niche breadth of generalists, and thus are more vulnerable to extinctions.

Here, we test whether diversification rates of New World Noctilionoidea, and particularly phyllostomids, are associated with specialization for frugivory, and how this pattern varies between mainland and the Antilles. For this, we first assessed whether mutualistic interactions could operate as a key innovation in the evolution of the group, and we also explored whether diversification might be driven by the shift to frugivory. Then we combined specialization for frugivory with other intrinsic (body size and length of forearm) and extrinsic (geographical range size and number of colonized ecoregions) factors to analyse the rate of diversification of this group of mammals.

## MATERIALS AND METHODS

### Taxonomic and geographical scope

The superfamily Noctilionoidea is composed of the families Myzopodidae from Madagascar, Mystacinidae from New Zealand and the New World families Noctilionidae, Furipteridae, Thyropteridae, Mormoopidae, and Phyllostomidae (Teeling *et al.*, 2005). We used the work of Teeling *et al.* (2005) as a reference for the supra-generic classification of bats. For generic and infra-generic taxa, we mainly followed the classification of Simmons (2005). We restricted the terms Antilles, West Indies and Caribbean to the islands of the Antillean Subregion as defined by Genoways *et al.* (1998).

### Reconstruction of the phylogeny and divergence time estimation

We estimated a time-calibrated phylogeny of the genera of New World Noctilionoidea from DNA sequences downloaded from GenBank (see Appendix S1 in Supporting Information). The genera *Amorphochilus*, *Lichonycteris*, *Neonycteris*, *Platalina*, *Scleronycteris* and *Xeronycteris* were not sampled because of a lack of sequences. They represent 9% of the genera and 3% of the species of the study group. The genera *Myzopoda* and *Mystacina* were used as outgroups in the phylogenetic reconstruction. The sampled genes were the nuclear recombination activating gene 2 (RAG2) and four mitochondrial genes: cytochrome *b* (*cyt b*) and the adjacent genes 12S rRNA, tRNA<sup>Val</sup> and 16S rRNA (the last three hereafter referred to as mitochondrial ribosomal DNA or mtrDNA).

We conducted individual alignments of the loci in MUSCLE 3.6 (Edgar, 2004) and we improved the alignment of mtrDNA in GBLOCKS 0.91b (Castresana, 2000). The general time-reversible model of substitution, with allowance for gamma distribution of rate variation and for some proportion of invariant sites (GTR +  $\Gamma$  + I), best fitted the data of each locus, as determined in jMODELTEST 0.1.1 (Posada, 2008). The phylogenetic reconstruction was conducted on concatenated sequences (4076 bases) previously partitioned by locus, and by codon position in the case of RAG2.

We performed the reconstruction of the phylogeny and the estimation of divergence dates in BEAST 1.6.1 (Drummond & Rambaut, 2007). We used the uncorrelated lognormal relaxed clock to account for lineage-specific rate heterogeneity (Drummond *et al.*, 2006) and the Yule process as the tree prior. Substitution models were unlinked for the three loci. We applied the GTR +  $\Gamma$  model with four rate categories to the mitochondrial loci. For RAG2, we used the Hasegawa–Kishino–Yano (HKY) +  $\Gamma$  model with four rate categories, with the first and second codon positions linked; the third positions were allowed to have a different relative rate of substitution, transition–transversion ratio and gamma distributed rate heterogeneity. Four calibration points were incorporated. Three of them included the lower limit of the Whitneyan stage (30.8 Ma; Morgan & Czaplewski, 2002) as minimum age

constraints of a lognormal distribution; the fourth included the lower limit of the Laventan stage (11.8 Ma; Czaplewski *et al.*, 2003). Maximum age constraints were set to the upper limit of divergence between Mystacinidae and New World Noctilionoidea (45.8 Ma), Noctilionidae and Furipteridae (35.7 Ma) and Mormoopidae and Phyllostomidae (40.99 Ma) (Teeling *et al.*, 2005). In the fourth case, we used the estimated upper limit of divergence between *Lophostoma* and *Mimon* (17.1 Ma; Hoffmann *et al.*, 2008). We conducted two independent analyses with 40 million steps, with sampling every 4000 steps. Convergence of the chain to the stationary distribution was confirmed by inspection of the Markov chain Monte Carlo samples in TRACER 1.5 (Rambaut & Drummond, 2007). The effective sample size of the parameters varied between 434 and 4992. We combined the last 4000 trees from each independent analysis. From the final sample of 8000 trees, we built a maximum clade credibility tree with the program TREEANNOTATOR 1.6.1. (<http://beast.bio.ed.ac.uk/TreeAnnotator>).

## Variables

We reviewed the literature to extend the database of feeding habits of Phyllostomidae (Rojas *et al.*, 2011) to the rest of the New World Noctilionoidea (see Appendix S2). We obtained data on body mass and forearm length from PanTHERIA (Jones *et al.*, 2009) and from other sources (e.g. Silva, 1979). Body mass and forearm length are two variables related to flight performance and foraging strategy in bats (Norberg & Rayner, 1987). We used the software gvsig 1.10 (<http://www.gvsig.org/web/>) and the spatial data collection of mammals held by the IUCN Red List website (<http://www.iucnredlist.org>; data downloaded on 1 November 2009) to build range maps and calculate range size of New World Noctilionoidea genera. We also used the Terrestrial Ecoregions Database hosted by the World Wildlife Fund website (<http://www.worldwildlife.org>; data downloaded on 30 October 2010) to determine the number of ecoregions colonized by each genus. Ecoregions are defined as units of land containing natural assemblages of taxa hierarchically structured into biomes and biogeographical realms with boundaries that approximate the original extent of assemblages prior to major land-use change (Olson *et al.*, 2001). We obtained data on extant species number per genus from Simmons (2005) and more recent literature (see Appendix S2).

## Phylogenetic analyses of diversification and comparative analyses of the correlates of diversity

Bat genera were classified as antagonistic (animalivorous and sanguinivorous) or mutualistic (nectarivorous and frugivorous). Although two of the six species of the genus *Chiroderma* are reported to be seed predators (Nogueira & Peracchi, 2003), we considered the genus as mutualistic because the bats disperse a small number of the ingested seeds intact. We also grouped the genera as non-frugivorous, complementary frugivorous, predominantly frugivorous or strictly frugivorous

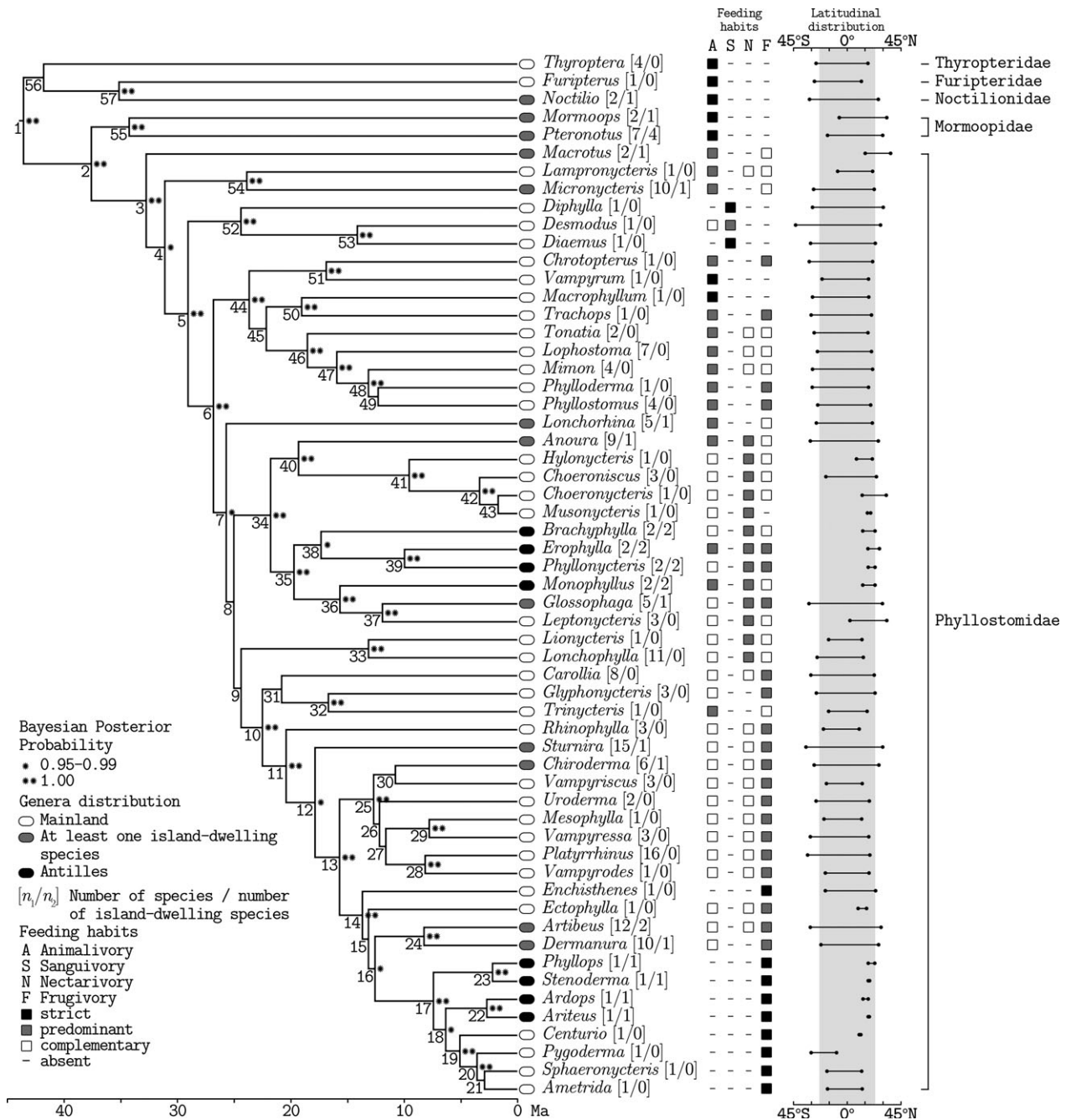
(Fig. 1). Detailed explanation of the dietary coding of bats at the genus level is available in Rojas *et al.* (2011).

We tested how diversification is driven by ecological role (i.e. antagonism or mutualism) across the time-calibrated phylogenetic tree with the binary state speciation and extinction model (BiSSE; Maddison *et al.*, 2007) corrected for incomplete phylogenies (FitzJohn *et al.*, 2009). This model simultaneously estimates speciation rates for antagonism ( $\lambda_0$ ) and mutualism ( $\lambda_1$ ), extinction rates for antagonism ( $\mu_0$ ) and mutualism ( $\mu_1$ ), and rate changes from antagonism to mutualism ( $q_{01}$ ) and vice versa ( $q_{10}$ ). On the same tree we tested how diversification is driven by specialization for frugivory with the multi-state speciation and extinction (MuSSE) model, which is a generalization of the BiSSE model. To test whether mutualism might have an effect on the rate of diversification of lineages we used an alternative model in which we constrained speciation rates of antagonists and mutualists to the same value (i.e.  $\lambda_0 = \lambda_1$ ). We then applied likelihood ratio tests to assess the performance of the unconstrained and constrained models. To conduct the analyses we specified an exponential prior (FitzJohn *et al.*, 2009) and computed the posterior probabilities of the parameters. We ran the models in the 'diversitree' package in R (<http://cran.r-project.org/web/packages/diversitree/index.html>).

The estimation of diversification rate of clades from phylogenetic data assumes that there are no limits on diversity, i.e. species number within clades increases unbounded through time. If this assumption is true we should expect a positive correlation between clade age and species richness (Rabosky, 2009a,b). According to Rabosky (2009a) the lack of such a correlation invalidates the use of diversification rates to understand species richness patterns, and in such cases the study should focus on factors influencing differences in species richness among clades, such as ecological factors limiting species richness (but see Wiens, 2011). We explored the relationship between the log-transformed number of species per genus (i.e. total clade diversification or  $\Omega$ , see below) and the stem age of the genus to detect whether older clades are more species-rich than younger clades (Gonzalez-Voyer *et al.*, 2011).

In addition to the total clade diversification (Rabosky, 2009a) we calculated the net rate of diversification for each lineage (i.e. the number of species that have accumulated per million years from the origin of the clade to the present) using the method-of-moment estimators of stem groups (Magallón & Sanderson, 2001), controlling for different values of the (unknown) extinction rate ( $\varepsilon = 0, 0.45, \text{ and } 0.90$ ). If the net rate of diversification is positively correlated with species richness, then diversification rates may help explain species richness patterns among clades (Wiens, 2011). If clade age and species richness are not related (see above) and rates of diversification are negatively correlated or uncorrelated with species richness, then either rates of diversification may be biased (Rabosky, 2009a,b) or they are not supported as an explanation for the diversity pattern in question, and this pattern could be explained by other factors (Wiens, 2011). When this happens, Gonzalez-Voyer *et al.* (2011) recommend using total clade diversification ( $\Omega$ ). We explored the





**Figure 1** Phylogenetic relationships, species richness, feeding habits and latitudinal distribution of New World Noctilionoidea genera. Values in the tree represent node numbers. For values of node support, divergence date estimates (in millions of years ago, Ma) and 95% highest posterior density limits (HPD) see Appendix S3.

relationship of total clade diversification and net rate of diversification with species richness. As we obtained similar results for the different values of  $\epsilon$  (see Appendix S3), only results for  $\epsilon = 0.45$  are presented. A previous simulation study indicated that diversification rate estimates are not sensitive to phylogenetic errors either in estimates of clade age or in topology (Wertheim & Sanderson, 2011), particularly when large sequences (> 4000 bases) are used to reconstruct the phylogeny, and when the phylogeny is calibrated with basal

fossils, as in our case. We used phylogenetic generalized least squares (PGLS) analyses (see Appendix S3) to quantify the relationships between variables (see Freckleton *et al.*, 2002).

Finally, we conducted a phylogenetic principal components analysis (PPCA) (Revell, 2009; see Appendix S3) on the mean values of the independent variables at the genus level (see below) to confront the multicollinearity problem previously detected with bivariate PGLS analyses. Specialization for frugivory, body mass, forearm length, geographical range size

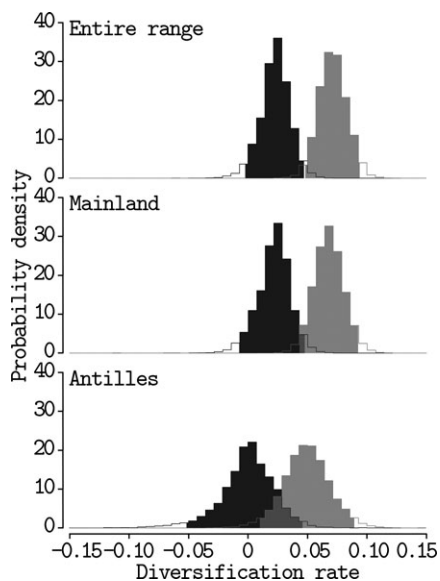
and number of colonized ecoregions were combined into five components. We used PGLS multiple regression analyses to identify correlates of the first two principal components with total clade diversification ( $\Omega$ ) and net diversification rate. The first two phylogenetic principal components account for 67% of the variation for the entire range as well as for the mainland, and account for 80% of the variation for the Antilles. We did not use the other components because of their low explanatory power. Assumptions of homoscedasticity and the distribution of residuals, corrected for phylogeny, were checked with diagnostic plots (Freckleton, 2009).

All analyses were performed for the full range of New World Noctilionoidea lineages and for mainland and Antillean lineages. In the latter two cases, the timetree obtained in BEAST was pruned to fit each biogeographical context, and the arithmetic mean of each independent variable was recalculated accordingly. We conducted the analyses with the PGLS code in the CAIC package for R (<http://r-forge.r-project.org/projects/caic>) using a significance level of 0.05.

## RESULTS

According to the phylogenetic reconstruction of the New World Noctilionoidea group, this clade began to diversify about 43.6 Ma (Fig. 1). The branching pattern and estimated times of divergence were consistent with previous works (Teeling *et al.*, 2005; Meredith *et al.*, 2011).

Diversification rates were higher in mutualistic than in antagonistic New World Noctilionoidea genera (Fig. 2). Mutualistic clades showed higher speciation rates and slightly lower extinction rates than antagonistic clades. This pattern was consistent for mainland and Antillean lineages, although in the latter case the extinction rate of mutualists was slightly



**Figure 2** Diversification rates of antagonistic (black) and mutualistic (dark grey) New World Noctilionoidea bats in different biogeographical contexts. The shaded areas correspond to the 95% credibility intervals of the posterior probability distributions.

higher than that of antagonists (Table 1). The constrained model of equal speciation rates ( $\lambda_0 = \lambda_1$ ) was rejected for the entire range ( $-2\Delta\ln L = 8.080$ ,  $\chi^2 = 8.073$ ,  $P = 0.004$ ; where  $\ln L$  is log-likelihood) and mainland ( $-2\Delta\ln L = 7.160$ ,  $\chi^2 = 7.165$ ,  $P = 0.007$ ), but not for the Antilles ( $-2\Delta\ln L = 3.178$ ,  $\chi^2 = 3.179$ ,  $P = 0.075$ ).

With regard to specialization for frugivory, only strictly frugivorous clades showed a higher diversification rate than the rest of the genera (Fig. 3). Apparently, facultative frugivory slightly increased diversification rates in both continental and Antillean mutualistic genera in comparison with animalivorous or insectivorous–nectarivorous lineages (Table 1). Extinction rates of strictly frugivorous clades were higher than those of the rest of the lineages, except in the Antilles where non-frugivorous clades showed a higher extinction rate than strictly frugivorous clades (Table 1).

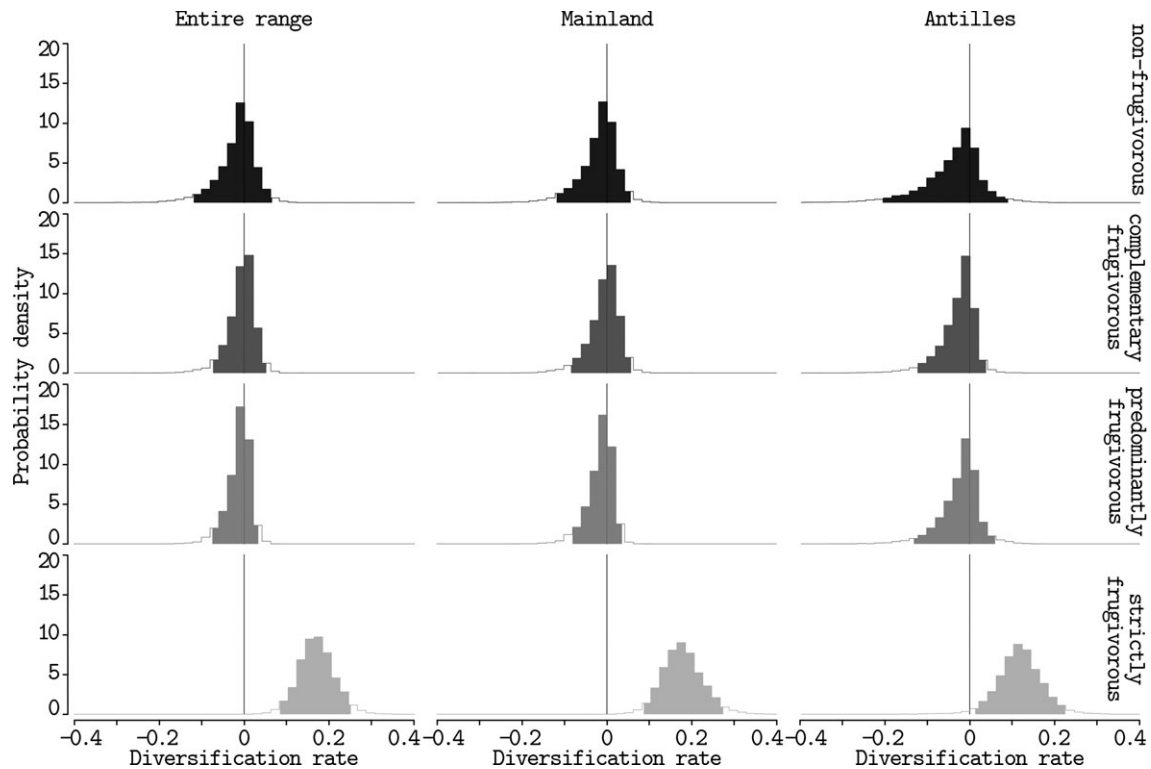
The log-transformed number of species per genus ( $\Omega$ ) was not significantly related to clade age (entire range  $r^2 = 0.043$ ,  $\beta = 0.008 \pm 0.005$ ,  $t_{56} = 1.588$ ,  $P = 0.118$ ; mainland  $r^2 = 0.009$ ,  $\beta = 0.004 \pm 0.006$ ,  $t_{48} = 0.643$ ,  $P = 0.523$ ; Antilles  $r^2 = 0.019$ ,  $\beta = -0.003 \pm 0.005$ ,  $t_{18} = -0.596$ ,  $P = 0.558$ ). The relationships of species richness and the estimates of rates of diversification were positive and significant in the three biogeographical contexts. Total clade diversification explained 87% of the variance of species richness in the entire range ( $\beta = 9.064 \pm 0.456$ ,  $t_{56} = 19.883$ ,  $P < 0.001$ ) and mainland ( $\beta = 8.881 \pm 0.495$ ,  $t_{48} = 17.929$ ,  $P < 0.001$ ) and 95% in the Antilles ( $\beta = 3.947 \pm 0.200$ ,  $t_{18} = 19.692$ ,  $P < 0.001$ ). Net rate of diversification explained 68% of the variance in the entire range ( $\beta = 107.646 \pm 9.828$ ,  $t_{56} = 10.953$ ,  $P < 0.001$ ) and mainland ( $\beta = 107.396 \pm 0.994$ ,  $t_{48} = 10.140$ ,  $P < 0.001$ ) and 59% in the Antilles ( $\beta = 25.493 \pm 11.304$ ,  $t_{18} = 5.049$ ,  $P < 0.001$ ). Total clade diversification and net rate of diversification were also strongly and significantly correlated (entire range  $r^2 = 0.734$ ,  $\beta = 10.349 \pm 0.832$ ,  $t_{56} = 12.432$ ,  $P < 0.001$ ; mainland  $r^2 = 0.718$ ,  $\beta = 11.004 \pm 0.994$ ,  $t_{48} = 11.065$ ,  $P < 0.001$ ; Antilles  $r^2 = 0.751$ ,  $\beta = 16.004 \pm 2.171$ ,  $t_{18} = 7.371$ ,  $P < 0.001$ ).

The model of correlates of total clade diversification in the entire range of New World Noctilionoidea explained 40% of the variance and was significant ( $F_{2,55} = 14.110$ ,  $P < 0.001$ ). The maximum likelihood of the  $\lambda$  parameter ( $\lambda_{ML}$ ) was  $< 0.001$ , significantly different from 1 ( $\chi^2 = 7.254$ ,  $P = 0.009$ ) but not from 0 ( $\chi^2 = -0.001$ ,  $P = 0.99$ ). The partial regression coefficient of the principal component  $z_1$  was significant, but this was not the case for  $z_2$  (Table 2). When we used net rate of diversification as the dependent variable, we obtained similar results [ $r^2 = 0.234$ ,  $F_{2,55} = 3.383$ ,  $P < 0.001$ ;  $\lambda_{ML} < 0.001$ , significantly different from 1 ( $\chi^2 = 27.069$ ,  $P < 0.001$ ) but not from 0 ( $\chi^2 = -0.0008$ ,  $P < 0.99$ )] (Table 2). The loadings on  $z_1$  of geographical range size ( $-0.898$ ), number of colonized ecoregions ( $-0.923$ ) and, to a lesser extent, specialization for frugivory ( $-0.318$ ) (Table 2) suggest that these variables were positively associated with diversification of noctilionoid bats.

For mainland lineages, the model of the first two phylogenetic principal components was significant and explained 34%

**Table 1** The effect of ecological role and specialization for frugivory on diversification of New World Noctilionoidea in different biogeographical contexts. Values indicate the proportion of Markov chain Monte Carlo (MCMC) runs from 1000 runs in which the differences in speciation ( $\lambda$ ), extinction ( $\mu$ ) and diversification ( $r$ ) rates followed the specified trend (e.g. 0.992 indicates that in 992 of the 1000 runs New World Noctilionoidea mutualists had higher speciation rates than antagonists). The number of taxa per biogeographical context (entire range/mainland/Antilles) is as follows: mutualist (45/37/15), antagonist (13/13/5), strictly frugivorous (9/5/4), predominant frugivorous (21/19/7), complementary frugivorous (17/15/6) and non-frugivorous (11/11/3).

	New World Noctilionoidea (entire range)			New World Noctilionoidea (mainland)			New World Noctilionoidea (Antilles)		
	$\lambda$	$\mu$	$r$	$\lambda$	$\mu$	$r$	$\lambda$	$\mu$	$r$
Ecological role									
Mutualist > antagonist	0.992	0.437	0.997	0.987	0.457	0.995	0.951	0.517	0.959
Specialization for frugivory									
Strictly frugivorous > non-frugivorous	1	0.590	0.999	1	0.585	0.999	0.974	0.454	0.967
Strictly frugivorous > complementary frugivorous	1	0.677	1	0.999	0.636	0.999	0.995	0.567	0.980
Strictly frugivorous > predominantly frugivorous	1	0.699	1	1	0.669	0.994	0.982	0.568	0.967
Predominantly frugivorous > non-frugivorous	0.359	0.390	0.517	0.375	0.407	0.510	0.420	0.388	0.561
Predominantly frugivorous > complementary frugivorous	0.335	0.469	0.431	0.282	0.465	0.399	0.565	0.494	0.540
Complementary frugivorous > non-frugivorous	0.521	0.420	0.574	0.589	0.456	0.591	0.358	0.387	0.531



**Figure 3** Diversification rates of New World Noctilionoidea bats according to the degree of specialization for frugivory. Results are shown for the entire range of the group and for mainland and Antillean lineages. The shaded areas (black, dark grey and light grey) correspond to the 95% credibility intervals of the posterior probability distributions.

of the variation of total clade diversification [ $F_{2,47} = 11.972$ ,  $P < 0.001$ ;  $\lambda_{ML} < 0.001$ , significantly different from 1 ( $\chi^2 = 13.879$ ,  $P < 0.001$ ) but not from 0 ( $\chi^2 = -0.001$ ,  $P < 0.99$ )]. The model using net rate of diversification as the dependent variable was also significant and explained 24% of

the variation of net rate of diversification [ $F_{2,47} = 7.383$ ,  $P = 0.002$ ;  $\lambda_{ML} < 0.001$ , significantly different from 1 ( $\chi^2 = 29.188$ ,  $P < 0.001$ ) but not from 0 ( $\chi^2 = -0.001$ ,  $P < 0.99$ )] (Table 2). In continental lineages, the increase in species richness and net rate of diversification was positively related to

**Table 2** Effect of specialization for frugivory and other intrinsic and extrinsic factors on species richness (log-transformed) and net diversification rates of New World Noctilionoidea genera in three biogeographical contexts. Number of taxa ( $n$ ), partial regression coefficients and standard errors ( $\beta \pm SE$ ), and values of the statistic ( $t$ -value) and their associated  $P$ -value are reported. Loadings of primary independent variables on each phylogenetic principal component ( $z$ ) are also provided. For the rest of the components see Appendix S3.

Biogeographical context	Species richness ( $\Omega$ ) as dependent variable				Net rate of diversification as dependent variable			
	Trait	$\beta \pm SE$	$t$	$P$	Trait	$\beta \pm SE$	$t$	$P$
Entire range ( $n = 58$ )	Intercept	0.362 $\pm$ 0.042	8.568	< 0.001	Intercept	0.021 $\pm$ 0.003	6.182	< 0.001
	$z_1$	-0.039 $\pm$ 0.007	-5.254	< 0.001	$z_1$	-0.0024 $\pm$ 0.0005	-4.059	< 0.001
	$z_2$	-0.011 $\pm$ 0.006	-1.661	0.102	$z_2$	-0.0006 $\pm$ 0.0005	-1.215	0.229
Mainland ( $n = 50$ )	Intercept	0.298 $\pm$ 0.049	6.138	< 0.001	Intercept	0.017 $\pm$ 0.004	4.390	< 0.001
	$z_1$	-0.040 $\pm$ 0.009	-4.607	< 0.001	$z_1$	-0.0024 $\pm$ 0.0007	-3.632	< 0.001
	$z_2$	0.020 $\pm$ 0.007	2.661	0.011	$z_2$	0.0012 $\pm$ 0.0006	2.052	0.046
Antilles ( $n = 20$ )	Intercept	0.119 $\pm$ 0.094	1.262	0.224	Intercept	0.004 $\pm$ 0.004	1.092	0.290
	$z_1$	-0.010 $\pm$ 0.004	-2.414	0.027	$z_1$	-0.0006 $\pm$ 0.0002	-2.969	0.009
	$z_2$	0.007 $\pm$ 0.006	1.072	0.299	$z_2$	-0.0006 $\pm$ 0.0004	1.646	0.118

Entire range:  $z_1 = -0.318$ (specialization for frugivory) + 0.075(body mass) - 0.095(forearm length) - 0.898(geographical range size) - 0.923(colonized ecoregions);  $z_2 = 0.057$ (specialization for frugivory) + 0.894(body mass) + 0.884(forearm length) + 0.080(geographical range size) - 0.079(colonized ecoregions).

Mainland:  $z_1 = -0.451$ (specialization for frugivory) - 0.058(body mass) - 0.342(forearm length) - 0.819(geographical range size) - 0.911(colonized ecoregions);  $z_2 = 0.159$ (specialization for frugivory) - 0.901(body mass) - 0.829(forearm length) + 0.240(geographical range size) + 0.074(colonized ecoregions).

Antilles:  $z_1 = 0.387$ (specialization for frugivory) - 0.866(body mass) - 0.812(forearm length) - 0.738(geographical range size) - 0.892(colonized ecoregions);  $z_2 = -0.019$ (specialization for frugivory) + 0.649(body mass) + 0.408(forearm length) - 0.454(geographical range size) - 0.563(colonized ecoregions).

geographical range size (loading = -0.819 on  $z_1$ ), exploitation of new ecoregions (loading = -0.911 on  $z_1$ ) and specialization for frugivory (loading = -0.451 on  $z_1$ ), and negatively associated with body mass and forearm length (loading = -0.901 and -0.829 on  $z_2$ , respectively).

For the Antillean lineages, the model of correlates of total clade diversification was not significant [ $r^2 = 0.291$ ,  $F_{2,17} = 3.489$ ,  $P = 0.054$ ;  $\lambda_{ML} = 0.999$ , neither significantly different from 1 ( $\chi^2 = 2.906$ ,  $P = 0.088$ ) nor from 0 ( $\chi^2 = -0.0002$ ,  $P = 0.99$ )], although the component  $z_1$  showed a significant and negative partial correlation coefficient ( $\beta^2 = -0.010 \pm 0.004$ ,  $P = 0.027$ ). On the contrary, the model of correlates of net rate of diversification was significant and explained 38% of the variation [ $F_{2,17} = 5.271$ ,  $P = 0.017$ ;  $\lambda_{ML} = 0.790$  neither significantly different from 1 ( $\chi^2 = 1.737$ ,  $P = 0.188$ ) nor from 0 ( $\chi^2 = 0.742$ ,  $P = 0.389$ )] (Table 2). Geographical range size, number of colonized ecoregions, body mass and forearm length were positively related to both species richness and diversification rates (loading = -0.738, -0.892, -0.866, and -0.812 on  $z_1$ , respectively). In contrast, there was a negative association of specialization for frugivory with the dependent variables (loading = 0.387 on  $z_1$ ).

## DISCUSSION

### Specialization for frugivory and diversification are evolutionarily linked

To our knowledge, our study is the first attempt to disentangle the relationship between frugivory and the

diversification of a monophyletic clade of mammals in a biogeographical framework. Our results show that frugivory is associated with diversification rates according to the biogeographical context: the association is positive in the mainland region and negative in the West Indies. Moreover, our results suggest that mutualistic interactions could play a role as a key innovation in the diversification of Neotropical noctilionoid bats.

Our results describe patterns rather than provide explanatory models. Nevertheless, we could examine the evidence suggesting that frugivorous bats may benefit directly from the mutualistic interaction per se, which might explain the role of frugivory in the diversification of bats. Phyllostomid bats not only facilitate regeneration of tropical forests by dispersing seeds of early successional shrubs and trees (Muscarella & Fleming, 2007) but also potentially increase the distribution ranges of the plant species (Albrecht *et al.*, 2007; Kelm *et al.*, 2008), positively influence the germination of seeds (Heer *et al.*, 2010) and probably also influence seedling recruitment of species with both small and large seeds (Melo *et al.*, 2009). In turn, composition, abundance, spatio-temporal patchiness and successional stage of plants producing fleshy fruits may determine the structure and evolution of Neotropical assemblages of frugivorous bats (Fleming *et al.*, 1987; Avila-Caballero *et al.*, 2009). If frugivorous bats favour the successional dynamics of the forest, enhance the germination of seeds and increase both the abundance and the range of plants producing fleshy fruits, then we could expect a positive feedback in the abundance and distribution of bat species, and therefore in the evolution of bat communities.



A key innovation is defined as the adaptive exploration of new ecological niches, following a novel structural character or physiological or functional innovations (Müller, 2002). Lack of support for equal rates of speciation between antagonists and mutualists and the results of the analyses of diversification driven by specialization for frugivory (see Fig. 3) suggest that frugivory was linked to a process of cladogenesis influenced by a key innovation (Hunter, 1998), at least in the evolution of continental lineages. The diversification of the order Chiroptera at the family level by the end of the Eocene was probably due to an increase in prey diversity (Teeling *et al.*, 2005). In this scenario of domination by insectivorous lineages, exploitation of fruits and flowers may have allowed diversification of mutualistic phyllostomid bats to occur during the Miocene (Rojas *et al.*, 2011), especially if this process was preceded by shifts to higher diversification rates of flowering plants (Davies *et al.*, 2004). Globally, Phyllostomidae (*c.* 159 species) and Pteropodidae (*c.* 190 species), the two bat families where phytophagy evolved as the main feeding habit, have reached a species richness as high as in the insectivorous Molossidae (*c.* 100 species) and Rhinolophidae (*c.* 162 species). All other insectivorous and animalivorous bat families (with the exception of Vespertilionidae) are less diverse at the species level (Simmons, 2005).

Monteiro & Nogueira (2011) examined the parallel evolution of mandibular shape and diet in phyllostomids and found a period of strong directional selection and divergence between 30 and 20 Ma. During this period, predominant frugivory was probably the main feeding habit in the most recent common ancestor of Carollinae, Glyphonycterinae, Rhinophyllinae, and Stenodermatinae (these subfamilies account for about 48% of the species of Neotropical noctilionoids), and complementary frugivory probably evolved in the most recent common ancestor of Glossophaginae and in the most recent common ancestor of the tribe Phyllostomini (Rojas *et al.*, 2011). Tests for correlated deviations in diversification rates of flowering plants and noctilionoid bats relative to a null model of constant lineage accumulation could be performed to assess the relationship between the radiation of phyllostomids and certain lineages of angiosperms (e.g. Solanaceae, Moraceae, Myrtaceae, Cactaceae, Arecaceae, Sapotaceae, Piperaceae, and Clusiaceae) that constitute important resources for frugivorous bats (see Muscarella & Fleming, 2007).

### Correlates of lineage diversification

We obtained a non-significant relationship between clade age and log-transformed species richness of New World noctilionoids. This suggests that age differences among noctilionoid lineages are not sufficient to explain differences in species richness. What other factors might explain such differences? Reduced variation in clade age among compared groups, positive correlation between speciation and extinction rates (i.e. clade volatility), ecological factors constraining species richness, and differences in rates of diversification influenced by species characteristics may explain the differences in species

richness in noctilionoids. Clade ages in New World Noctilionoidea show relatively high variation, between 43.62 and 1.73 Ma (see Fig. 1 and Appendix S3); however, both relatively younger (e.g. *Platyrrhinus*, *Artibeus*, *Dermanura*) and older (e.g. *Pteronotus*, *Micronycteris*) lineages show high numbers of extant species, which does not support the prediction of the clade volatility hypothesis of younger lineages being more species-rich than older clades because the latter would be pruned by extinction (Gilinsky, 1994). Although we cannot discard the effect of extinction in older clades in shaping the pattern of species richness of New World noctilionoid bats, our results show that both extrinsic and intrinsic species traits of species have contributed to lineage diversification.

We found that geographical range size and number of ecoregions were strongly and positively related to species richness and net rate of diversification of continental and insular lineages (see Table 2). Additionally, range size and number of colonized ecoregions do not differ significantly for bat genera with different degrees of specialization for frugivory (see Appendix S3). Larger areas usually support more resources and appropriate habitats and therefore can provide ecological opportunities for diversification (MacArthur & Wilson, 1967; Yoder *et al.*, 2010). Range size is also related to the number of physical barriers encountered that could promote allopatric speciation (Rosenzweig, 1995). Colonization of new ecoregions could be considered analogous to the occupation of new adaptive zones and might lead to shifts in dietary niche, possibly favouring diversification (Hunter, 1998). The colonization of new ecoregions may operate in conjunction with the shift to frugivory as an ecological opportunity that ultimately leads to speciation (Yoder *et al.*, 2010). This process even applies to the Antilles, which has a much lower diversity of ecoregions than the mainland. Island area and island elevation (both responsible for higher habitat diversity) are highly correlated with bat species richness in the West Indies (Willig *et al.*, 2009). Correlations of species richness with island area, island elevation and habitat diversity have also been found in Antillean butterflies, reptiles and birds (Morand, 2000). Perhaps, the strongest evidence for the positive effect of geographical range size and number of ecoregions on the diversification of frugivorous bats comes from the strictly frugivorous bats (subtribe Stenodermatina). The estimate of divergence times of this clade suggests that during the Miocene a continental ancestor reached the Antilles and started to diversify in isolation, giving rise to the *Phyllops–Stenoderma* (*c.* 5.2 Ma, node 23 in Fig. 1) and *Ardops–Ariteus* (*c.* 4.7 Ma, node 22 in Fig. 1) clades; then, in the Pliocene, an Antillean ancestor dispersed to the continent and, faced with many ecoregions and a much greater area, diversified over the course of approximately 2 million years into the genera *Centurio*, *Pygoderma*, *Sphaeronycteris* and *Ametrida* (see Fig. 1, Appendix S3). With the exception of *Centurio*, the distribution ranges of continental Stenodermatina are threefold larger than those of related Antillean genera.

Body size is linked to dispersal abilities, resource requirements, ecological interactions and niche partitioning. Previous

evidence indicates that body size is not correlated with species richness across the order Chiroptera (Isaac *et al.*, 2005). According to our analysis, there is an opposite relationship of body mass and forearm length with diversification rates: negative in the mainland and positive in the West Indies. This pattern could be related to the different selective pressures on optimal body size between mainland and island systems. In mainland communities, interspecific interactions (especially predation and competition) facilitate evolutionary divergence from the optimum body size for energy acquisition. In islands or continental island-like ecosystems, selection favours evolutionary convergence to optimal size (Lomolino, 2005; but see Raia *et al.*, 2010). In islands, a reduction in mass is a way to reduce energy expenditure. For example, the bats *Monophyllus redmani* and *Erophylla sezekorni*, endemic to the Bahamas and Greater Antilles, have basal metabolic rates that are 1.73 times lower than those of their continental counterparts (McNab, 2009). Nevertheless, the rate of energy expenditure in island bats can also vary independently of mass (see the revision in McNab, 2009). Dispersal abilities could explain the positive relationship between body size and diversification of insular lineages. Larger species might be able to reach more areas and colonize ecoregions where different selective pressures and unexploited ecological opportunities might ultimately lead to speciation events. Range size and maximal body mass were not correlated in mainland lineages ( $\beta = 2.266 \pm 2.146$ ,  $t_{48} = 1.056$ ,  $P = 0.296$ ) but were marginally correlated in Antillean lineages ( $\beta = 0.225 \pm 0.110$ ,  $t_{18} = 2.041$ ,  $P = 0.056$ ).

### The effect of islands and latitudinal distribution on diversification of bats

The Antilles imposed differences on the rate of diversification of antagonistic lineages. Contrary to the mainland pattern, the extinction rate of mutualistic Antillean noctilionoids was slightly higher than the extinction rate of antagonists (see Table 1), but the diversification rate of antagonists had a negative value (see Fig. 2) because the speciation rate of Antillean antagonistic noctilionoids was lower than the speciation rate of mutualists. In other words, apparently the West Indies have not favoured the diversification of animalivorous noctilionoid bats. This statement should be contrasted with the fossil record of Antillean bats, which is currently scarce, as is that of the rest of the order (Rodríguez-Durán & Kunz, 2001).

In addition, the role of mutualism as a key innovation for island-dwelling bats was not supported in our analysis. This could be related to the negative relationship of specialization for frugivory to total clade diversification and net rate diversification of island-dwelling lineages. Specialization for frugivory, on the contrary, was positively correlated with diversification rates of mainland lineages. The limitation of resources on the islands may operate against the evolutionary success of strictly frugivorous bats promoting, by contrast, the evolutionary adaptation of lineages that act not only as seed dispersers but also as flower-pollinating and insect-consuming

agents, which is the case with *Erophylla*, *Phyllonycteris*, and *Monophyllus* (Soto-Centeno & Kurta, 2006; Mancina & Herrera, 2010). Strictly frugivorous Antillean genera are currently monotypic and restricted to a few islands, while the genera less specialized for fruit consumption (*Brachyphylla*, *Erophylla*, *Phyllonycteris*, and *Monophyllus*) are each composed of two species and are distributed across the West Indies (Willig *et al.*, 2009). Furthermore, as stated above, specialized lineages might be more vulnerable to extinction in insular environments. For example, the genus *Artibeus* comprises 12 extant species of predominant frugivores and only one fossil species, *Artibeus anthonyi*, from Cuba (Silva, 1979). In contrast, the genus *Phyllops*, which comprises one extant strictly frugivorous species (*Phyllops falcatus*), distributed in Cuba, Hispaniola, Grand Cayman, and Cayman Brac, also includes two extinct species from Cuba (*Phyllops silvai* and *Phyllops vetus*), whose cranial morphology suggests they were also strict frugivores (Suárez & Díaz-Franco, 2003).

The positive relationship of specialization for frugivory with total clade diversification and net rate diversification in continental noctilionoids might be confounded with the effect of the latitudinal distribution of the genera. If frugivorous bats (i.e. strictly and predominantly frugivorous genera) are currently confined to tropical areas, whereas non-frugivorous bats occur in both tropical and temperate regions, then higher diversification of frugivores was probably caused by: (1) the physical and ecological conditions of the tropics (e.g. higher temperature, climatic stability, larger area with regard to temperate regions, higher likelihood of parapatric and sympatric speciation), (2) by greater time-for-speciation in tropical regions (tropical habitats have existed much longer than temperate ones), or (3) by both (Wiens & Donoghue, 2004; Mittelbach *et al.*, 2007; Wiens, 2011). Consequently, the role of the shift to frugivory in the evolution of the group could be overstated herein. Nevertheless, most continental noctilionoid genera have overlapping latitudinal distributions (see Fig. 1). This spatial pattern does not deny the effect of a mechanism other than dietary shifts explaining the diversification of the group in the mainland (Stevens, 2011), but suggests that, whatever the mechanism, it would have had the same probability to operate on both non-frugivorous and frugivorous clades.

### CONCLUSIONS

In conclusion, the shift to frugivory during the evolution of Neotropical noctilionoids was positively associated with diversification rates of continental lineages and negatively related to diversification of island-dwelling genera. Other important extrinsic and intrinsic factors were positively associated with diversification of noctilionoids in both biogeographical scenarios. We focused on specialization for frugivory and classified noctilionoid genera accordingly. Nevertheless, we propose that further studies that focus on the spatial and evolutionary patterns of species richness of noctilionoids must include a comprehensive classification of

food habits. Whether this classification may change what we know so far from the classical classification of piscivory–insectivory–sanguivory–carnivory–nectarivory–frugivory is debatable, but we consider that incorporating in the analyses the complexity of mixed feeding habits of phyllostomids might provide a more integrative approach (McNab, 2003). Finally, our study suggests that land-use changes that reduce the distinctiveness of ecoregions would threaten the diversity of New World noctilionoids, compromising the ecosystem services provided by flower-pollinating and seed-dispersing bats and especially jeopardizing the animalivorous bat species of the Antilles.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** GenBank accession numbers for the taxa included in this research.

**Appendix S2** Taxonomic and dietary information for New World Noctilionoidea.

**Appendix S3** Phylogenetic analyses.

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## BIOSKETCHES

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Author contributions: D.R. conceived the ideas; D.R. and A.V. collected the data; D.R., V.F., A.V. and L.N. analysed the data; and D.R. and L.N. led the writing.

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