

Extinctions, traits and phylogenetic community structure: insights from primate assemblages in Madagascar

Onja H. Razafindratsima, Siya Mehtani and Amy E. Dunham

O. H. Razafindratsima (onja@rice.edu), S. Mehtani and A. E. Dunham, Rice Univ., Dept of Ecology and Evolutionary Biology, MS 170, 6100 Main St., Houston TX 77005. OHR also at: Centre ValBio BP 33, Ranomafana, Ifanadiana 312, Madagascar.

Understanding the origin and maintenance of community composition through ecological and evolutionary time has been a central challenge in ecology. However little is known about how extinction may alter patterns of phylogenetic and phenotypic structure within communities. To address this, we used past and present primate communities in Madagascar as our model system to explore how a large extinction event within a taxon may alter evolutionary relationships and phenotypic distributions within communities. We also explored the influence of environment on the structure of present-day lemur communities. We found a phylogenetic pattern of overdispersion in both past and present-day communities. However, trait structures, including relative dispersion of body masses and trophic niches were altered following extinction. We posit that the overdispersed phylogenetic patterns have resulted from the unique ecological and evolutionary history of Madagascar's primates including a rapid adaptive radiation in the presence of a broad niche-space available during colonization. Differences in trait structures between present and past primate communities may be reflective of the selective extinction process that eliminated the largest primates from the island. Habitat also appeared to influence the structure of present-day lemur communities. Lower divergence in patterns of phylogeny, body mass and activity rhythms were found in dry relative to wet habitats. This may be due to potential advantages of being small and nocturnal in environments with low productivity and hot dry climates. We suggest current studies exploring community processes should consider potential effects of past extinction events. Such work is important for understanding community assembly, coexistence, and mechanisms driving extinctions, particularly given the current extinction crisis facing ecosystems globally.

Ecologists have long sought to understand the origin and maintenance of community composition through ecological and evolutionary time (Darwin 1859, Elton 1946). The interactions between species in a given community and between species and their environment may be important drivers in the process of community assembly (Darwin 1859) and may result in patterns or signatures of phenotypic and phylogenetic similarities (Webb et al. 2002, Ingram and Shurin 2009). Since phenotypic trait similarities are often strongly correlated with phylogenetic relatedness, incorporating phylogeny has recently gained great interest for analyzing community assembly, along with ecological and historical factors (Webb et al. 2002, Sargent and Ackerly 2008, Graham et al. 2009).

There are three main mechanisms often discussed in recent studies as potential drivers of patterns of community assembly. Darwin (1859) considered that 1) competition and 2) environmental filtering may result in contrasting patterns of community assembly, and more recently, researchers have considered the potential importance of 3) random processes (Connor and Simberloff 1979, Hubbell 2001). If competition is a driving factor, closely related species are expected to be unable to coexist because of their high

ecological similarity which may lead them to compete too strongly for resources (Cardillo et al. 2008, Cooper et al. 2008, Cavender-Bares et al. 2009). This situation would favour a community with a higher level of trait-state diversity and phylogenetic separation than one would expect by a random assemblage (overdispersion, Fox 1987, 1999, Webb et al. 2002). The opposite pattern is expected in the case of environmental filtering, under which habitat characteristics select for species that share certain adaptive traits allowing them to persist in that environment. This situation is thus expected to result in a lower trait state diversity and less phylogenetic separation than expected by random assemblage (under-dispersion or clustering, Webb et al. 2002). When chance processes such as dispersal drive assembly (Hubbell 2001) or multiple factors oppose and nullify each other, communities will resemble a random assemblage in both phenotypic and phylogenetic distribution.

Evolutionary and colonization history may also be important. For example, the niche width available to a certain taxa group relative to their diversity may also affect the level of divergence of traits (Roughgarden 1974) and therefore phylogenetic distance within a community. In addition, monophyletic lineages that have undergone rapid adaptive

radiation in a region are expected to display phenotypic and phylogenetic overdispersion (Cavender-Bares et al. 2006).

Primate communities have recently been used to test community assembly rules as a model taxon (Cooper et al. 2008, Kamilar 2009, Kamilar and Guidi 2010, Beaudrot and Marshall 2011) since comprehensive global data on community composition and species ranges of this taxon are better known than any other vertebrate taxon. Primates show a general pattern of random assemblage (Kamilar and Guidi 2010) that appears to be mostly driven by dispersal (Beaudrot and Marshall 2011) consistent with the neutral theory of community assembly (Hubbell 2001). However, primate communities in Madagascar (comprised of endemic lemurs) are unique in showing strong patterns of phylogenetic overdispersion (Kamilar and Guidi 2010) and niche differentiation (Beaudrot and Marshall 2011). It has been suggested by several authors (Richard and Dewar 1991, Ganzhorn 1997, Burney et al. 2004, Kamilar and Guidi 2010) that the current pattern of lemur community structure may be strongly influenced by the recent stepwise cascade of extinctions involving numerous primates after human arrival two millennia ago (Burney et al. 2004). Extinct taxa include many sympatric congeners which held similar traits such as large body size and folivorous diets. Thus, the loss of these species has been proposed as a potential driver of the current pattern of overdispersion and niche differentiation within communities not found in other land masses, where recent extinctions of similar magnitude have not occurred (Kamilar and Guidi 2010). Madagascar's primates are also on the verge of a new extinction event, with a majority of species currently threatened from habitat destruction, hunting and/or climate change (Randrianandianina et al. 2003, Dunham et al. 2008, 2011). Thus understanding how extinction might alter community structure is particularly relevant for this region.

Madagascar's primates also differ from other primates in their evolutionary history. Lemurs underwent rapid diversification from a single common ancestor on an island that was missing the high diversity of mammalian and avian fauna that compete with primates elsewhere (Yoder and Yang 2004, Karanth et al. 2005). This wide niche space and rapid diversification could also explain the divergent phenotypic and phylogenetic structures of present-day lemur communities.

Another potentially important factor for community formation that might lead to variation in patterns of community structure across Madagascar is environment. Lemurs inhabit a vast array of environments from montane rainforest to spiny desert habitat. Frequent droughts, high temperatures, high elevations and certain habitat types may constrain community membership. Thus lemur communities may be useful for examining the potential impacts of habitat filtering on both phenotypic and phylogenetic structure of communities.

Our goals were to look at how extinction may have altered patterns of Malagasy primate assemblages, and to explore possible effects of environmental filtering related to rainfall, temperature, habitat type and elevation on phylogenetic- and trait-structure of Madagascar's present-day primate communities. We approached this goal by examining the associations between phylogenetic assemblages and trait similarities within present-day and Holocene lemur communities in forest regions across Madagascar. We also explored associations of habitat characteristics with phylogenetic

distance and trait similarity measures in present-day communities. We predicted that if large-scale extinction has resulted in the divergent structural patterns of lemur communities then the present-day assemblages will show higher overdispersion in phylogeny and divergence of traits than past communities. Overdispersion in both past and present communities would be predictive of other mechanisms such as the evolutionary history of lemurs on Madagascar. We also predicted that environmental filtering will be stronger in areas with lower rainfall, higher temperatures, or higher elevation such that communities in these habitats will display less divergent traits and less overdispersed phylogenies.

Methods

Community composition

The present-day lemur communities in our study were determined by compiling a database of lemur species presence/absence in 44 protected areas of Madagascar (Fig. 1, Supplementary material Appendix 1). We define a community as the occurrence of more than one primate species living sympatrically in one geographical location (Reed and Bidner 2004, Kamilar and Guidi 2010). Communities with three or less species were excluded from the analysis to avoid misinterpreting the large number of ties between observed and null communities (Webb et al. 2008).

Our Holocene communities were adopted from Godfrey et al. (1997a) and Godfrey and Jungers (2002) and additional communities were reconstructed from the literature based on the distribution of subfossil lemur species in 18 localities (Wunderlich et al. 1996, Godfrey et al. 1997a, b, Godfrey and Jungers 2003, Gommery et al. 2004). Subfossil sites of Holocene communities were matched to corresponding sites of present day communities by selecting protected areas nearest the subfossil sites and < 100 km away. We did this by georeferencing the subfossil location map in Godfrey et al. (1997b) onto a map of modern forest cover using ArcGIS 10.0. Composition of the Holocene communities in our study (Supplementary material Appendix 1) included all subfossil and extant (some locally extinct) lemur species found in Madagascar's rich subfossil record (Ganzhorn 1997, Godfrey et al. 1997a, 1999). While we assumed this method was robust, it is not flawless and we recognize the uncertainty in reconstructing any past community. Thus, results involving community reconstructions always require some careful interpretation, although we expect general patterns to be upheld.

Phylogeny construction

The phylogeny used in this study included 68 extant and 16 extinct lemur species and was constructed using as a template the phylogenetic tree of primate taxa published by Horvath et al. (Horvath et al. 2008) which contained 24 extant lemur species. A supertree inferred from the template and other phylogenetic trees (Del Pero et al. 1995, 2006, Montagnon et al. 2000, 2001, Pastorini et al. 2001, 2002, Roos et al. 2004, Karanth et al. 2005, Horvath and Willard 2007,

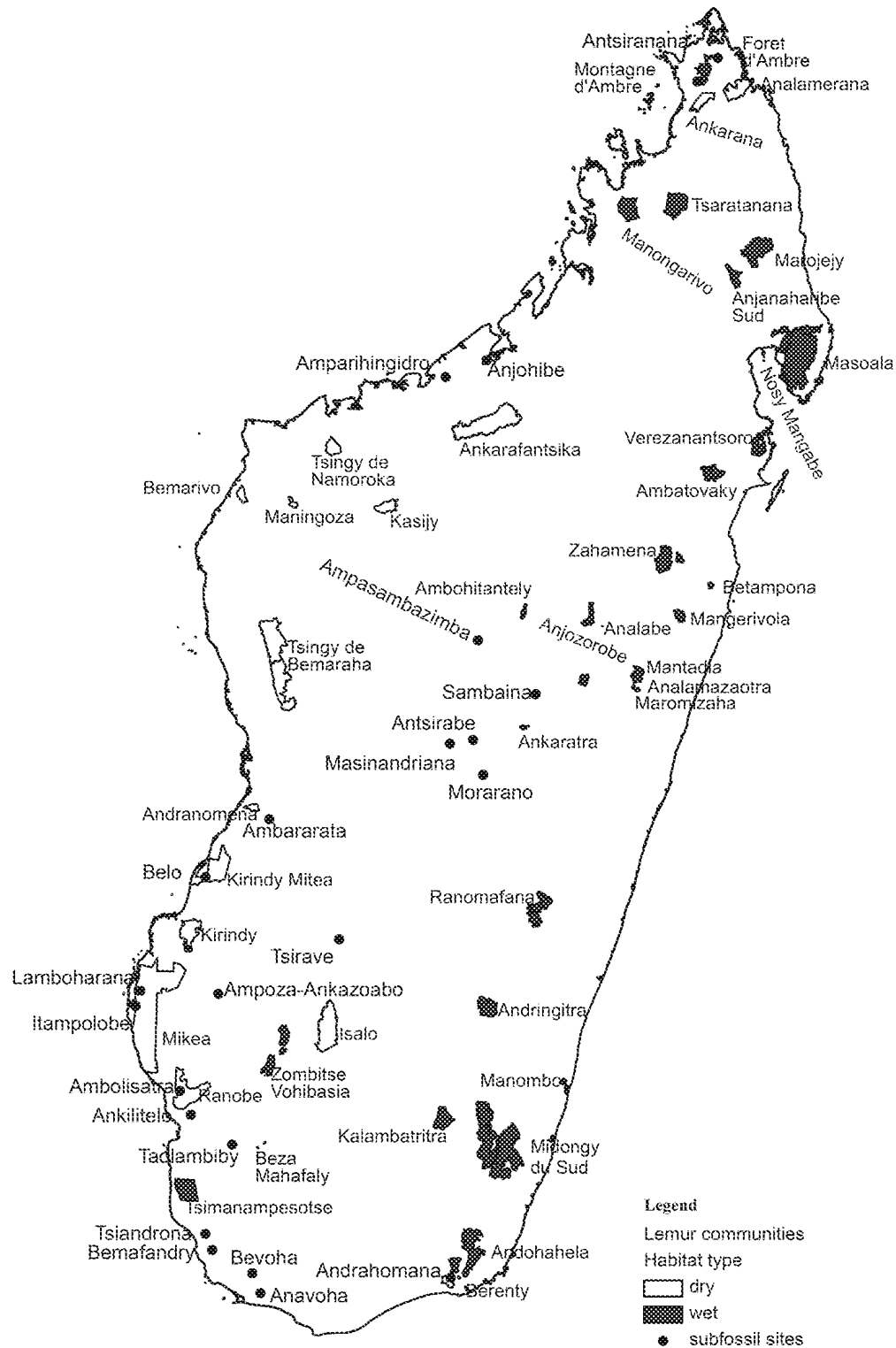


Figure 1. Distribution of the Malagasy primate communities in this study.

Orlando et al. 2008, Catlett et al. 2010) was created with 'bladj' method in Phylocom ver. 4.1 (Webb et al. 2008). These two trees were used to reconstruct a more complete phylogenetic tree using 'comnode' procedure in Phylocom ver. 4.1 (Webb et al. 2008). We used Mesquite ver. 2.72 (Maddison and Maddison 2002–2009) to create the Nexus file of the phylogeny and for visual representation (Fig. 2).

Community phylogenetic structure

For each community, we measured the standardized effect size of phylogenetic community structure by calculating two phylogenetic metrics using Phylocom ver. 4.1 (Webb et al. 2008): net relatedness index (NRI) and nearest taxon index (NTI) (Webb et al. 2002). NRI measures the mean



Figure 2. Phylogenetic tree of Malagasy primates reconstructed from Horvath et al. (2008). Scale used: million years.

phylogenetic distance (MPD) between all species pairs in a community (MPD_{sample}) relative to the mean phylogenetic distance of all taxa in a null community ($MPD_{\text{rndsample}}$),

standardized by the standard deviation of phylogenetic distances in the null communities, $sd(MPD_{\text{rndsample}})$. It is calculated as follows:

$$NRI_{\text{sample}} = -1 \times \frac{MPD_{\text{sample}} - MPD_{\text{rndsample}}}{sd(MPD_{\text{rndsample}})}$$

NTI is based on the mean nearest phylogenetic neighbour distance (MNND), and is used to determine if the most closely related species in a community are more related than expected by chance alone. It is calculated in the same way as NRI by replacing MPD by MNND as follows:

$$NTI_{\text{sample}} = -1 \times \frac{MNND_{\text{sample}} - MNND_{\text{rndsample}}}{sd(MNND_{\text{rndsample}})}$$

Negative values of these metrics indicate that closely related taxa co-occur less than expected by chance, positive values indicate that they co-occur more often than expected by chance, and values near zero indicate a random assemblage of nearest neighbours. NRI and NTI are complementary in explaining the overall pattern of community structure. While a deep level of conservatism will give high values of NRI and NTI, clustering primarily at the terminal branches in the phylogeny will result in a higher NTI relative to NRI (Webb et al. 2002). We used t-tests and Wilcoxon signed-rank (for non-normal distributions) to determine whether the mean of the distribution across communities for NTI and NRI differed from zero demonstrating a general trend towards either clustering or overdispersion.

Null communities were generated by maintaining the number of species within each community but randomizing the identity of occurring species in each sample (Webb et al. 2008). For each null community, species were drawn without replacement from a pool of all species on the island for a total of 9999 randomizations. Separate species pools were used for present-day and Holocene communities. The number of species in each community and the number of communities inhabited by each species was the same in real and null communities. The advantage of maintaining species' frequencies across communities is that it makes our tests less sensitive to interspecific differences that might make some species more common across sites including dispersal and colonization ability (Stone et al. 2000); the disadvantage is that it is less sensitive to the effects of competitive ability that might also affect species commonness across sites (Brown et al. 2002).

Trait structure of communities

We collected, from the literature, trait characteristics, which were thought to be potentially important for competition among lemurs including mean body mass, diet, and activity rhythm (Supplementary material Appendix 2). Lemur taxa are generally sexually monomorphic in body mass (Dunham and Rudolf 2009), thus body mass was representative of both sexes within species. Activity rhythm was classified into three classes: diurnal, nocturnal and cathemeral; and diet into five classes: folivore, frugivore, insectivore, gummivore and omnivore (Godfrey et al. 2004, Mittermeier et al. 2006). Extant species were assigned a particular diet category if the diet contained > 50% of such items; if species consumed multiple resources with no resource > 50% they were

considered omnivores (Ganzhorn 1997). The diet categories assigned to extinct species were based on features such as dental crown morphology, cranial architecture, dental development and electron scanning microwear and through analogy to nearest extant relatives (Godfrey et al. 1997a).

For community patterns of body mass, we calculated the mean pairwise trait distance among taxa (MPTD) within each community. This represents the mean difference of the trait value between all species pairs within a community. We also calculated the mean nearest trait distance (MNTD), which represents the mean difference of the trait value between each species within a community. High values indicate limiting similarity (Weiher and Keddy 1995, Schamp et al. 2010) and smaller values indicate trait convergence (Grime 2006, Schamp et al. 2010).

For diet and activity rhythm we measured the richness (number of types) and evenness (a measure of the relative abundance of types, where dominance leads to lower evenness scores) of the traits represented within each community sample, and tested it against that expected in corresponding null communities (described previously). A richness and or evenness higher than expected by chance suggests evidence of limiting similarity and lower values than expected by chance indicate that some categories may be favoured over others within a certain habitat (Schamp et al. 2010). Evenness was calculated as follows (Pielou 1974):

$$j = \frac{-\sum p_i \log p_i}{\log S}$$

where S is the richness of the trait in the sample and p_i the proportion of each trait-category in the sample.

We used the standardized effect size (SES) of the trait indices (MPTD, MNTD, Richness, and Evenness) to look for patterns of trait dispersion in the communities. $SES = (I_{\text{sample}} - I_{\text{null}}) / sd_{\text{null}}$, where I_{sample} is the observed index, I_{null} is the mean of the randomized community and sd_{null} is its standard deviation (Gotelli and Ellison 2002, Ernst and Rödel 2006). Standardizing the effect size is essential because it removes the bias effect of sample size and therefore even with different sample size the effects can be comparable (Rosenthal 1994, Jennions and Moller 2003, Nakagawa 2004). Significant difference from zero would indicate an overall tendency toward clustering (negative values) or higher dispersion/evenness (positive values) of traits relative to the pattern expected by chance (Ingram and Shurin 2009).

Effects of habitat characteristics

We collected data on environmental features including maximum elevation, habitat type (dry vs wet), minimum rainfall and mean and maximum temperature for the 44 protected areas where the communities in our study were located (Supplementary material Appendix 3). We chose these variables because they are often associated with physiological tolerances or resource availability and thus have potential to constrain community composition through environmental filtering. We tested for differences in species richness between wet vs dry habitat types to ensure similar levels of diversity and found no significant difference ($F = 1.47$,

DF = 43, $p = 0.23$). These data were then used to test for associated patterns of phylogenetic and trait structure of the present-day communities relative to habitat features using least-square linear regression analyses. These analyses were not done with the Holocene communities because of possible recent changes to these habitat features.

Results

Phylogenetic structure of communities

Supporting previous studies on primates (Kamilar 2009, Kamilar and Guidi 2010), a majority of present-day lemur communities in our study displayed phylogenetic overdispersion, indicating that individuals were more distantly related than expected by chance. This pattern however was only observed at the tips of the phylogenies as demonstrated through the nearest taxon index (NTI) (Table 1). We found that 72.7% of present-day communities displayed a negative NTI, indicating phylogenetic overdispersion of nearest neighbors. Similar overdispersion patterns were not observed with the net relatedness index (NRI) which looks at phylogenetic distance of all species pairs in the community (Table 1).

The Holocene communities demonstrated a similar pattern with phylogenetic overdispersion at the tips of the phylogeny (NTI: Table 1), with 72.2% of communities demonstrating negative NTI values. Like the present-day communities, this pattern of overdispersion within communities did not hold when distance patterns were examined across the whole phylogeny of the communities (NRI: Table 1). There was no significant difference in either measure of phylogenetic distance pattern when the Holocene communities were compared to their corresponding present-day communities (Table 1) indicating that extinction has not significantly altered phylogenetic structure of these communities.

Trait structure of communities

Body mass distribution of present-day lemurs across communities was not different than expected by chance for measures between pairs matched by nearest trait values (SES-MNTD)

and among all species pairs community (SES-MPTD) (Table 2). However, within the Holocene communities, there was more divergence of body mass for closest species pairs relative to that expected by chance (Table 2).

Diet was found to be more evenly distributed (lack of dominant or rare diets) among present-day lemur communities than expected by chance, and dietary diversity was higher in the present-day communities than expected by chance (Table 2). However, for the Holocene communities, diet was randomly distributed and there were no more or less diet types than expected by chance (Table 2).

Lemur activity rhythms were found to be more evenly distributed among the present-day lemur communities than a random assemblage but richness of activity rhythms did not differ from random (Table 2). The same patterns were observed for the Holocene communities (Table 2).

Habitat characteristics and community structure

Patterns of phylogenetic relatedness for present-day taxa did not differ according to major habitat categorization (wet forest vs dry forest), elevation or temperature variables (Table 1). NRI decreased in association with higher minimum rainfall suggesting more overdispersion in wetter habitats but NTI was not associated with rainfall levels (Table 1).

None of the environmental variables (rainfall, elevation, temperature) was associated with divergence patterns of body mass among lemur communities (Table 2). However, taxa in drier habitats were more similar to each other than were those in wet habitats (Table 2). Results indicated that diet structures of the present-day communities were not affected by the environmental variables or habitat type (Table 2).

Outcomes of associations between activity rhythm distributions and habitat characteristics of communities were varied. We found no association between the standardized effect size (SES) of richness of activity rhythm and minimum rainfall or maximum elevation of the area (Table 2). However there was a significant relationship between the SES of richness of activity rhythm and major habitat type (Table 2) with the wet habitat being richer than dry. The SES values of richness account for the differing sample sizes between communities, avoiding potential sampling effects.

Table 1. Overall distribution pattern (from zero value) of the measures of phylogenetic structure across past and present-day lemur communities, and least-square linear regression analyses of the associated patterns of phylogenetic structure of the present-day communities relative to habitat features (SR: Wilcoxon signed-rank values, min: minimum, max: maximum, rain: rainfall, temp: temperature; significance is represented by an asterisk and bold).

	NRI	NTI
Communities		
holocene	$t = 0.853$, DF = 17, $p = 0.609$	SR = -57.5, DF = 17, $p = 0.010^*$
present-day	SR = -143.0, DF = 43, $p = 0.096$	SR = -309.0, DF = 43 $p < 0.001^*$
holocene vs present-day	$Z = -0.11330$, DF = 1, $p = 0.910$	$t = -1.341$, DF = 29.67, $p = 0.190$
Environmental variables		
min rain	$R^2 = 0.108$, DF = 42, $p = 0.031^*$	$R^2 = 0.027$, DF = 42, $p = 0.291$
max elev	$R^2 = 0.001$, DF = 42, $p = 0.997$	$R^2 = 0.045$, DF = 42, $p = 0.174$
mean temp	$R^2 = 0.007$, DF = 43, $p = 0.585$	$R^2 = 0.030$, DF = 43, $p = 0.262$
max temp	$R^2 = 0.001$, DF = 43, $p = 0.878$	$R^2 = 0.017$, DF = 43, $p = 0.403$
habitat type	$t = -1.905$, DF = 42, $p = 0.064$	$t = -0.882$, DF = 42, $p = 0.383$

Table 2. Distribution pattern of the measures of trait structure within past and present-day lemur communities (min: minimum, max: maximum, rain: rainfall, temp: temperature; bold and asterisk represent significant values, subscript represent degree of freedom).

	Body mass		Diet		Activity rhythm	
	SES_MNTD	SES_MPTD	SES_evenness	SES_richness	SES_evenness	SES_richness
holocene	$t_{13} = 4.92$ $p < 0.001^*$	$T_{13} = 0.11$ $p = 0.911$	$t_{17} = 0.19$ $p = 0.848$	$t_{17} = 1.80$ $p = 0.091$	$t_{17} = 8.25$ $p < 0.001^*$	$t_{17} = -1.66$ $p = 0.115$
present-day	$t_{38} = -0.47$ $p = 0.630$	$t_{38} = -0.61$ $p = 0.540$	$t_{43} = 5.82$ $p < 0.001^*$	$t_{43} = 2.75$ $p = 0.009^*$	$t_{43} = 4.92$ $p < 0.001^*$	$t_{43} = -1.63$ $p = 0.111$
min rain	$R^2 = 0.002$ DF = 38 $p = 0.794$	$R^2 = 0.088$ DF = 42 $p = 0.054$	$R^2 = 0.001$ DF = 42 $p = 0.879$	$R^2 = 0.038$ DF = 42 $p = 0.212$	$R^2 = 0.025$ DF = 42 $p = 0.315$	$R^2 = 0.043$ DF = 42 $p = 0.123$
max elev.	$R^2 = 0.002$ DF = 38 $p = 0.812$	$R^2 = 0.002$ DF = 43 $p = 0.798$	$R^2 = 0.035$ DF = 42 $p = 0.227$	$R^2 = 0.021$ DF = 42 $p = 0.350$	$R^2 = 0.003$ DF = 42 $p = 0.741$	$R^2 = 0.036$ DF = 42 $p = 0.225$
max temp	$R^2 = 0.050$ DF = 39 $p = 0.165$	$R^2 = 0.016$ DF = 43 $p = 0.409$	$R^2 = 0.007$ DF = 43 $p = 0.596$	$R^2 = 0.016$ DF = 43 $p = 0.416$	$R^2 = 0.043$ DF = 43 $p = 0.177$	$R^2 = 0.036$ DF = 43 $p = 0.411$
mean temp	$R^2 = 0.005$ DF = 39 $p = 0.669$	$R^2 = 0.008$ DF = 43 $p = 0.570$	$R^2 = 0.013$ DF = 43 $p = 0.215$	$R^2 = 0.016$ DF = 43 $p = 0.409$	$R^2 = 0.040$ DF = 43 $p = 0.700$	$R^2 = 0.009$ DF = 43 $p = 0.542$
habitat type	$t = -1.57$ DF = 39 $p = 0.125$	$t = -2.33$ DF = 42 $p = 0.025^*$	$t = -0.02$ DF = 42 $p = 0.987$	$t = -1.62$ DF = 42 $p = 0.112$	$t = -1.34$ DF = 42 $p = 0.187$	$t = 2.87$ DF = 42 $p = 0.006^*$

Discussion

Extinction resulting from human activities has altered species assemblages in many ecosystems, affecting both diversity and phylogenetic structure of communities (Winter et al. 2009, Turvey and Fritz 2011). However generally, very little is known about how large-scale extinctions are likely to affect trait structures or the patterns of evolutionary relationships within communities. Large extinction events are often not random, and tend to affect specialized endemic or rare species, often from species-poor families with life history traits that tend to respond to environmental change (Sechrest et al. 2002). Global mammalian assemblages show a phylogenetic and phenotypic clustering in both past extinctions and current extinction risks, including Madagascar's fauna (Turvey and Fritz 2011).

Large body mass is associated with high extinction risk especially in the tropical regions (Fritz et al. 2009). Depending on how these species are distributed across and within communities will determine how they might alter phylogenetic and phenotypic structure. Madagascar experienced a large scale extinction of megafauna that occurred from the late Holocene to as recently as 500 yr ago (Karanth et al. 2005) and is among the island that has the highest Holocene mammal extinctions (Turvey and Fritz 2011). It has been suggested that these extinctions may be the reason for the current overdispersion in phylogenetic relationships and higher levels of niche differentiation found in communities of lemurs relative to other primate assemblages (Richard and Dewar 1991, Ganzhorn 1997, Burney et al. 2004, Kamilar and Guidi 2010).

Using data from the literature on community compositions of primates in Madagascar during the Holocene, and in present-day communities, we tested the prediction that past extinction events resulted in present-day communities with lower phylogenetic relatedness and higher trait divergence than past assemblages. While we did not find that extinctions

of lemurs during the late Holocene altered the current overall phylogenetic structure of lemur communities, we did find changes in patterns of traits within communities.

Community phylogenetic structure

Our results suggest that the extinction of many lemur species in Madagascar did not seem to alter the phylogenetic structure of lemur communities overall. The majority of both present-day and Holocene communities were found to be phylogenetically overdispersed assemblages with species more distantly related than expected by chance. The extinction of large species thus does not seem to be responsible for the difference in phylogenetic structure of the Malagasy primate assemblages.

We suggest that the pattern of phylogenetic dispersion in Madagascar may instead be a result of the ecological and evolutionary history of lemurs on the island. Lemurs diversified from a single common ancestor that colonized the island from Africa in the early Tertiary period (Yoder and Yang 2004, Karanth et al. 2005). On an island with a relatively depauperate mammalian and avian community to compete with, they then underwent rapid adaptive radiation and diversified into a taxon with a remarkable diversity of morphologies and life histories. For a monophyletic lineage with a broad niche width available allowing for rapid adaptive radiation, it is expected that competition will result in a high level of trait divergence (Roughgarden 1974) and communities may become more phenotypically and phylogenetically more divergent than expected by chance (Cavender-Bares et al. 2006) as found in the lemur communities. In Africa, Asia and the Neotropics, competition appears to have played less of a role in structuring primate communities and dispersal appears to be more important (Beaudrot and Marshall 2011). However, substantial competition with other vertebrates during their diversification may mask strong effects

of competition in structuring these communities because of the exclusion of non-primates from these studies (Beaudrot and Marshall 2011).

Trait structure of communities

Based on the lemur's evolutionary history as described above, the trait structures of their communities might also be expected to show more divergent patterns relative to random. Among present-day communities, this prediction held for both diet and activity rhythm, but not for body mass which appeared random. However, when Holocene communities were examined, they showed greater divergence in body mass than expected by chance. This was the opposite pattern to what was predicted by previous studies, but the same mechanism may hold (Richard and Dewar 1991, Ganzhorn 1997, Burney et al. 2004, Kamilar and Guidi 2010). The difference between present-day and Holocene communities may be due to selective pressures resulting in the extinction of the largest species of lemurs, which may have been a result of a combination of factors including human hunting, climatic changes, and habitat loss (Godfrey and Irwin 2007). Interestingly, the diet assemblage in the Holocene communities was random which differs from the divergent diet composition of the present-day communities. Since extinct species' diets are reconstructions and not observations, we cannot rule out that uncertainty of diet may have influenced our results. However, if these reconstructions of general diet type are accurate, we speculate that the larger body size of the extinct species may have allowed these frugivores and folivores to exploit different niches within their guild (larger fruits, or lower quality forage afforded by larger body size), thus reducing competition and allowing coexistence. Present day lemurs fall within a much smaller range of body sizes for which competition may be more intense and coexistence may be more likely among species in more divergent diet categories.

Habitat characteristics and community structure

Although previous work by Kamilar and Muldoon (2010) showed no relationship between climatic niches (including temperature and rainfall) with phylogenetic distance in lemurs, our results suggest environmental factors may play a role in the phylogenetic structuring of communities. We found that lemur phylogenetic structure was not affected by elevation or temperature variables; however, we noted more overdispersion of communities in areas with higher minimum rainfalls and in the eastern rainforest habitats than in the dry western habitats. It is possible that the dry conditions and lower productivity associated with the dry habitats (Ganzhorn et al. 1997) act as a filter such that more specialization may be required for inhabiting these environments thus reducing the role of competition in structuring communities in these regions. While Kamilar (2009) found no difference in phylogenetic structuring between these two regions (with a smaller sample size of communities), a later paper (Kamilar and Ledogar 2011) found that within guilds

there was less structuring of communities in the western dry habitats and their interpretation was consistent with ours in terms of environmental filtering.

Trait structures of the communities support this idea with the exception of diet. Activity rhythms and body masses were less divergent in dry habitats than in the wet habitats. Dry habitats in Madagascar tend to have smaller bodied lemurs, a possible adaptation to the lower environmental productivity in those habitats (Albrecht et al. 1990). They also tend to have a higher ratio of nocturnal species which may be a thermoregulatory and/or osmoregulatory adaptation to the hot, dry daytime of these climates.

Conclusions

Species extinction is a natural process as well as a growing conservation concern for biodiversity which is facing increasing anthropogenic pressures worldwide. However, studies of phylogenetic and phenotypic community structure have largely ignored the potential influence of past extinction events on present-day patterns (Winter et al. 2009). Such studies are useful for understanding the processes of assembly, coexistence and speciation within communities (Cavender-Bares et al. 2009) but are also important for targeting conservation actions to preserve evolutionary history within communities (Purvis et al. 2005), and for helping us understand mechanisms driving extinctions. Understanding how patterns of community structure are altered by extinction is of increasing importance given the current extinction crisis faced by ecosystems globally (Avice et al. 2008), and especially in conservation 'hotspots' such as Madagascar (Myers et al. 2000), which is also a model region of species diversification (Vences et al. 2009). Our results suggest that past extinction events in Madagascar have resulted in structural changes in phenotypic but not phylogenetic patterns of diversity in Madagascar based on comparisons of Holocene with present-day primate communities. Further research is needed to understand how current anthropogenic pressures including climate change, deforestation or exotic species invasion may alter future patterns of phenotypic and phylogenetic diversity in Madagascar and elsewhere and how we might prevent such changes. Extinction is often tied to vulnerabilities of specific life-history traits (often linked to phenotypic traits like body size) to natural and human-induced environmental change (Sechrest et al. 2002). These traits in turn can be selected out of communities resulting in reduced diversity and altered community structure. In Madagascar, many of the future extinctions could be prevented by expanding and maintaining existing protected areas and creating protected corridors to link remnant fragments and to encourage dispersal (Lehman 2006).

Acknowledgements – Thanks to K. Whitney and J. Rudgers and to participants in the Fall 2009 Rice EEB Community Phylogenetics seminar for providing helpful suggestions and feedback. OHR was supported by The Leakey Foundation, Philanthropic Educational Organization and Schlumberger Foundation fellowships. Special thanks to Maria Meza-Lopez and Mamy-Fy Rakotondrainibe for their help in collecting data.

References

- Albrecht, G. H. et al. 1990. Ecogeographic size variation among the living and subfossil prosimians of Madagascar. – *Am. J. Phys. Anthropol.* 22: 1–50.
- Avise, J. C. et al. 2008. In the light of evolution II: biodiversity and extinction. – *Proc. Natl Acad. Sci. USA* 105: 11453–11457.
- Beaudrot, L. H. and Marshall, A. J. 2011. Primate communities are structured more by dispersal limitation than by niches. – *J. Anim. Ecol.* 80: 332–341.
- Brown, J. H. et al. 2002. Assembly rules and competition in desert rodents. – *Am. Nat.* 160: 815–818.
- Burney, D. A. et al. 2004. A chronology for late prehistoric Madagascar. – *J. Hum. Evol.* 47: 25–63.
- Cardillo, M. et al. 2008. Global patterns in the phylogenetic structure of island mammal assemblages. – *Proc. Natl Acad. Sci. USA* 275: 1549–1556.
- Catlett, K. K. et al. 2010. “Life history space”: a multivariate analysis of life history variation in extant and extinct Malagasy lemurs. – *Am. J. Phys. Anthropol.* 142: 391–404.
- Cavender-Bares, J. et al. 2006. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. – *Ecology* 87: 109–122.
- Cavender-Bares, J. et al. 2009. The merging of community ecology and phylogenetic biology. – *Ecol. Lett.* 12: 693–715.
- Connor, E. F. and Simberloff, D. 1979. The assembly of species communities: chance or competition? – *Ecology* 60: 1132–1140.
- Cooper, N. et al. 2008. A common tendency for phylogenetic overdispersion in mammalian assemblages. – *Proc. Natl Acad. Sci. USA* 275: 2031–2037.
- Darwin, C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. – *J. Murray.*
- Del Pero, M. et al. 1995. Phylogenetic relationships among Malagasy lemurs as revealed by mitochondrial DNA sequence analysis. – *Primates* 36: 431–440.
- Del Pero, M. et al. 2006. A composite molecular phylogeny of living lemuroid primates. – *Folia Primatol.* 77: 434–445.
- Dunham, A. E. and Rudolf, V. H. W. 2009. Evolution of sexual size monomorphism: the influence of passive mate guarding. – *J. Evol. Biol.* 22: 1376–1386.
- Dunham, A. E. et al. 2008. Evaluating effects of deforestation, hunting, and El Niño events on a threatened lemur. – *Biol. Conserv.* 141: 287–297.
- Dunham, A. E. et al. 2011. Global climate cycles and cyclones: consequences for rainfall patterns and lemur reproduction in southeastern Madagascar. – *Global Change Biol.* 17: 219–227.
- Elton, C. 1946. Competition and the structure of ecological communities. – *J. Anim. Ecol.* 15: 54–68.
- Ernst, R. and Rödel, M. O. 2006. Community assembly and structure of tropical leaf-litter anurans. – *Ecotropica* 12: 113–129.
- Fox, B. J. 1987. Species assembly and the evolution of community structure. – *Evol. Ecol.* 1: 201–213.
- Fox, B. J. 1999. The genesis and development of guild assembly rules. – In: Weiher, A. and Keddy, P. (eds), *Ecological assembly rules: perspectives, advances, retreats.* Univ. of Cambridge Press, pp. 23–57.
- Fritz, S. A. et al. 2009. Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. – *Ecol. Lett.* 12: 538–549.
- Ganzhorn, J. U. 1997. Test of Fox’s assembly rule for functional groups in lemur communities in Madagascar. – *J. Zool.* 241: 533–542.
- Ganzhorn, J. U. et al. 1997. Habitat characteristics and lemur species richness in Madagascar. – *Biotropica* 29: 331–343.
- Godfrey, L. R. and Jungers, W. L. 2002. Quaternary fossil lemurs. – In: Hartwig, W. C. (ed.), *The primate fossil record.* Cambridge Univ. Press, pp. 97–121.
- Godfrey, L. R. and Jungers, W. L. 2003. The extinct sloth lemurs of Madagascar. – *Evol. Anthropol.* 12: 252–263.
- Godfrey, L. R. and Irwin, M. T. 2007. The evolution of extinction risk: past and present anthropogenic impacts on the primate communities of Madagascar. – *Folia Primatol.* 78: 405–419.
- Godfrey, L. R. et al. 1997a. Subfossil lemurs: inferences about past and present primate communities in Madagascar. – In: Goodman, S. and Patterson, B. (eds), *Natural change and human impact in Madagascar.* Smithsonian Inst. Press, pp. 218–256.
- Godfrey, L. R. et al. 1997b. Reappraisal of the postcranium of *Hadropithecus* (Primates, Indroidea). – *Am. J. Phys. Anthropol.* 103: 529–556.
- Godfrey, L. R. et al. 1999. Past and present distributions of lemurs in Madagascar. – In: Rakotosamimanana, B. et al. (eds), *New directions in lemur studies. Proceeding of the XVIIth Congress of the International Primatological Congress, New York,* pp. 19–53.
- Godfrey, L. R. et al. 2004. Ontogenetic correlates of diet in Malagasy lemurs. – *Am. J. Phys. Anthropol.* 123: 250–276.
- Gommery, D. et al. 2004. Nouvelle découverte dans le Nord-Ouest de Madagascar et répartition géographique des espèces du genre *Palaeopropithecus*. – *Ann. Paléontol.* 90: 279–286.
- Gotelli, N. J. and Ellison, A. M. 2002. Assembly rules for New England ant assemblages. – *Oikos* 99: 591–599.
- Graham, C. H. et al. 2009. Phylogenetic structure in tropical hummingbird communities. – *Proc. Natl Acad. Sci. USA* 106: 1265–1277.
- Grime, P. J. 2006. Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. – *J. Veg. Sci.* 17: 255–260.
- Horvath, J. E. and Willard, H. F. 2007. Primate comparative genomics: lemur biology and evolution. – *Trends Genet.* 23: 173–182.
- Horvath, J. E. et al. 2008. Development and application of a phylogenomic toolkit: resolving the evolutionary history of Madagascar’s lemurs. – *Genome Res.* 18: 489–499.
- Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography.* – Princeton Univ. Press.
- Ingram, T. and Shurin, J. B. 2009. Trait-based assembly and phylogenetic structure in northeast Pacific rockfish assemblages. – *Ecology* 90: 2444–2453.
- Jennions, M. D. and Moller, A. P. 2003. A survey of the statistical power of research in behavioral ecology and animal behavior. – *Behav. Ecol.* 14: 438–445.
- Kamilar, J. M. 2009. Environmental and geographic correlates of the taxonomic structure of primate communities. – *Am. J. Phys. Anthropol.* 139: 382–393.
- Kamilar, J. M. and Guidi, L. M. 2010. The phylogenetic structure of primate communities: variation within and across continents. – *J. Biogeogr.* 37: 801–813.
- Kamilar, J. M. and Muldoon, K. M. 2010. The climatic niche diversity of Malagasy primates: a phylogenetic perspective. – *PloS One* 5: e11073.
- Kamilar, J. M. and Ledogar, J. A. 2011. Species co-occurrence patterns and dietary resource competition in primates. – *Am. J. Phys. Anthropol.* 144: 131–139.
- Karanth, K. P. et al. 2005. Ancient DNA from giant extinct lemurs confirms single origin of Malagasy primates. – *Proc. Natl Acad. Sci. USA* 102: 5090–5095.
- Lehman, S. M. 2006. Conservation biology of Malagasy Strepsirrhines: a phylogenetic approach. – *Am. J. Phys. Anthropol.* 130: 238–253.

- Maddison, W. P. and Maddison, D. R. 2002–2009. Mesquite: a modular system analysis for evolutionary analysis, version 2.72. – <<http://mesquiteproject.org>>.
- Mittermeier, R. A. et al. 2006. Conservation international tropical field guide series: lemurs of Madagascar. – Washington DC Conservation International.
- Montagnon, D. et al. 2000. Ancient DNA from *Megaladapis edwardsi* (Malagasy subfossil): preliminary results using partial cytochrome b sequence. – *Folia Primatol.* 72: 30–32.
- Montagnon, D. et al. 2001. Taxonomic relationships and sampling effects among Lepilemuridae and Lemuridae using a partial cytochrome b gene. – *Comptes Rendus de l'Academie des Sciences Series III Sciences de la Vie* 324: 647–656.
- Myers, N. et al. 2000. Biodiversity hotspots for conservation priorities. – *Nature* 403: 853–858.
- Nakagawa, S. 2004. A farewell to Bonferroni: the problems of low statistical power and publication bias. – *Behav. Ecol.* 15: 1044–1045.
- Orlando, L. et al. 2008. DNA from extinct giant lemurs links archaeolemurids to extant indriids. – *BMC Evol. Biol.* 8: 121–129.
- Pastorini, J. et al. 2001. Phylogenetic history of sifakas (*Propithecus*: Lemuriformes) derived from mtDNA sequences. – *Am. J. Phys. Anthropol.* 53: 1–17.
- Pastorini, J. et al. 2002. Phylogenetic relationships among Lemuridae (Primates): evidence from mtDNA. – *J. Hum. Evol.* 43: 463–478.
- Pielou, E. C. 1974. Population and community ecology principles and methods. – Gordon and Breach Science Publishers.
- Purvis, A. et al. 2005. Phylogeny and conservation. – Cambridge Univ. Press.
- Randrianandianina, B. N. et al. 2003. The role of protected areas in the management of the island's biodiversity. – In: Goodman, S. M. and Benstead, J. P. (eds), *The natural history of Madagascar*. Univ. of Chicago Press, pp. 1423–1432.
- Reed, K. E. and Bidner, L. R. 2004. Primate communities: past, present and possible future. – *Am. J. Phys. Anthropol.* 47: 2–39.
- Richard, A. F. and Dewar, R. E. 1991. Lemur ecology. – *Annu. Rev. Ecol. Syst.* 22: 145–175.
- Roos, C. et al. 2004. Primate jumping genes elucidate strepsirrhine phylogeny. – *Proc. Natl Acad. Sci. USA* 101: 10650–10654.
- Rosenthal, R. 1994. Parametric measures of effect size. – In: Cooper, H. and Hedges, L. V. (eds), *The handbook of research synthesis*. Russell Sage Foundation, pp. 231–244.
- Roughgarden, J. 1974. Niche width: biogeographic patterns among *Anolis* lizard populations. – *Am. Nat.* 108: 429–442.
- Sargent, R. D. and Ackerly, D. D. 2008. Plant–pollinator interactions and the assembly of plant communities. – *Trends Ecol. Evol.* 23: 123–130.
- Schamp, B. et al. 2010. Deterministic assembly of land snail communities according to species size and diet. – *J. Anim. Ecol.* 79: 803–810.
- Sechrest, W. et al. 2002. Hotspots and the conservation of evolutionary history. – *Proc. Natl Acad. Sci. USA* 99: 2067–2071.
- Stone, L. et al. 2000. On desert rodents, favored states, and unresolved issues: scaling up and down regional assemblages and local communities. – *Am. Nat.* 156: 322–328.
- Turvey, S. T. and Fritz, S. A. 2011. The ghosts of mammals past: biological and geographical patterns of global mammalian extinction across the Holocene. – *Phil. Trans. R. Soc. B* 366: 2564–2576.
- Vences, M. et al. 2009. Madagascar as a model region of species diversification. – *Trends Ecol. Evol.* 24: 456–465.
- Webb, C. O. et al. 2002. Phylogenies and community ecology. – *Annu. Rev. Ecol. Syst.* 33: 475–505.
- Webb, C. O. et al. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. – *Bioinformatics* 24: 2098–2100.
- Weihner, E. and Keddy, P. A. 1995. Assembly rules, null models, and trait dispersion: new questions from old patterns. – *Oikos* 74: 159–164.
- Winter, M. et al. 2009. Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. – *Proc. Natl Acad. Sci. USA* 106: 21721–21725.
- Wunderlich, R. E. et al. 1996. New pedal remains of *Megaladapis* and their functional significance. – *Am. J. Phys. Anthropol.* 100: 115–138.
- Yoder, A. D. and Yang, Z. 2004. Divergence dates for Malagasy lemurs estimated from multiple gene loci: geological and evolutionary context. – *Mol. Ecol.* 13: 757–773.

Supplementary material (Appendix E7409 at <www.oikosoffice.lu.se/appendix>). Appendix 1–3.