

# Understanding Primate Communities: Recent Developments and Future Directions

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In 1999, the edited volume *Primate Communities* presented several studies that examined broad-scale patterns of primate diversity.<sup>1</sup> Similar studies were being conducted on nonprimate taxa; advances in data availability and statistical approaches were allowing scientists to investigate a variety of new questions and to reexamine classical questions in novel ways. While such studies on nonprimate taxa have continued at a steady pace, they have only crept forward for primate species (Fig. 1). In the intervening time, the field of macroecology (Box 1) rapidly developed and has resulted in several books<sup>2–4</sup> and the establishment of new research institutes. We suggest that examining primate communities, especially in a macroecological context, is an important line of research for our field to embrace and an area where biological anthropologists can provide major contributions. We review the current state of research, describe new datasets and research tools, and suggest future research directions.

Primates are a key to understanding ecological and biogeographic differences among tropical forest regions because they are commonly found in these areas and are a major

component of vertebrate biomass.<sup>5</sup> The distribution of primates has been well-studied because they are more easily and accurately censused than any other mammalian forest taxa due to their typically diurnal activity patterns, relatively large bodies, and noisy group-living behavior.<sup>6</sup> Moreover, primates exhibit intra- and interspecific variation in a range of biological traits, which makes them an excellent reference point for comparative studies that can inform principles of ecology and biogeography<sup>7–9</sup> and provide insight into such areas as the macroecology of body size,<sup>10,11</sup> density,<sup>12</sup> abundance,<sup>13</sup> and geographic range size.<sup>14</sup>

multivariate techniques to compare variation in the ecological niches primates occupy across regions. Two studies expanded this research by investigating the ecological consequences of potential primate extinctions<sup>17</sup> and the connection between plant productivity and primate species richness in the Neotropics.<sup>18</sup>

Similar and complementary approaches to studying primate community ecology culminated in the book, *Primate Communities*,<sup>1</sup> which remains a must-read for anyone interested in primate community ecology, macroecology, and biogeography. The edited volume begins with a series of chapters describing primate communities in Africa, Asia, Madagascar, and the Neotropics in terms of their species composition, habitat use, biomass, and resources used. The later sections provide several broad comparisons of primate communities across regions. Major findings include a consistently positive relationship between phylogenetic divergence and ecological distance, inverse relationships between both species richness and biomass and population density and biomass, an important influence of phylogeny on primate social systems, and correlations between primate and mammalian species richness across regions. Finally, several studies highlight the inescapable and influential role of humans, particularly through hunting, on primate communities around the world.

In 2004, Reed and Bidner<sup>19</sup> systematically reviewed the existing knowledge about primate communities. This included a review of the effects of historical factors, climate and habitat, plant productivity, food

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Key words: macroecology; biogeography; community ecology; primatology; mammal; paleo-communities; species coexistence; species distributions; interspecific competition

## WHAT DO WE KNOW?

Early quantitative examinations of broad-scale variation in primate communities were published by Kaye Reed and John Fleagle.<sup>15,16</sup> For the first time, these studies investigated drivers of primate species richness, including forest cover area and mean annual rainfall, and used

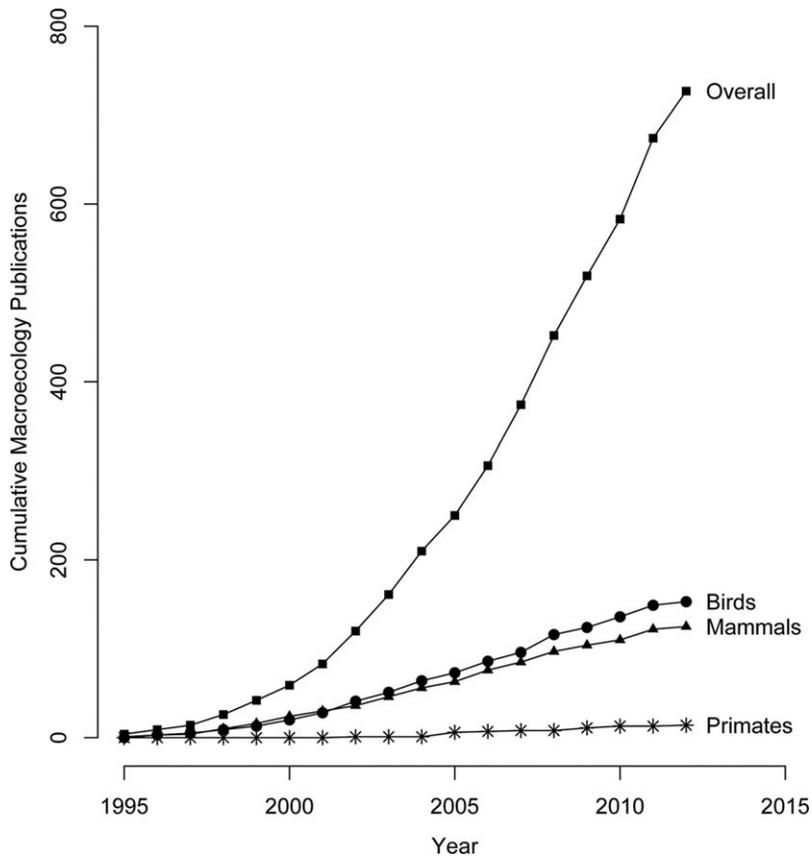


Figure 1. Cumulative macroecology publications over time (through August 2012). We performed key word searches using ISI Web of Science to examine the growth in macroecology research across taxa following the initial use of the term in 1995. Taxa were defined as overall ("macroecology"), primates ("macroecology and primates"), mammals ("macroecology and mammals not primates"), and birds ("macroecology and birds").

resources and species interactions on primate communities around the globe. The review also provided questions for future research, some of which remain unanswered today. For example, what has caused the relatively low primate species richness in Asia? How will the loss of predators affect primate communities? How effective are corridors for maintaining primate metacommunities? Why do polyspecific associations occur in some regions and some forests but not others? Other questions highlighted by Reed and Bidner have since received attention. For example, they asked why is there an abundance of folivorous primates in Madagascar and a paucity of folivorous primates in the Neotropics? Ganzhorn and associates<sup>20</sup> have demonstrated differences between regions with respect to nitrogen levels in fruit. They suggest that the low

concentration of protein in Malagasy fruits may have driven selection in some lemurs for adaptations to process difficult to digest but protein-rich foods, such as leaves, whereas high protein levels in Neotropical fruits were likely sufficient.

Although *Primate Communities* and the subsequent review were landmark publications, there was not (with a few exceptions<sup>21–24</sup>) an immediate increase in research on primate community ecology. Within the last five years, however, there appears to have been a growing interest in primate community and macroecology. Traditionally, studies in community ecology have focused on understanding the processes affecting community composition at the local scale, particularly interactions between species, such as plant-animal interactions, predation, and competition,<sup>25,26</sup> whereas macroecological studies have

examined regional- and continental-level patterns, such as spatial turnover in community composition (that is, beta diversity) and the underlying ecological and evolutionary processes that drive these patterns, such as speciation and dispersal.<sup>27</sup>

### Primate Communities at the Local Scale

Recent research in community ecology has expanded our understanding of local-scale interactions between primate species and their environment. Several studies have documented how the loss of primate species will affect other trophic levels, particularly in terms of primates' ecological role of dispersing seeds.

A case study at Kibale forest in Uganda suggested that the removal of primates could lead to declines in plant seedling richness and density.<sup>28</sup> Stevenson<sup>29</sup> found a consistent relationship between ateline primate density and plant diversity across 16 Neotropical sites, suggesting that as atelines are reduced through hunting, plant diversity declines due to a reduction in seed dispersal. Plant diversity also declines when large-bodied seed-dispersing primates are extirpated by human hunting.<sup>30,31</sup> Some experimental evidence suggests that loss of tropical seed dispersers such as primates will result in the reduction of some plant species over time.<sup>32</sup>

Community level analyses within a study site have led to new developments in our understanding of interactions between primates and their predators. Lwanga and colleagues<sup>33</sup> report the first documented case of a long-term primate population decline (red colobus) due to predation by another primate species (chimpanzee). Their data, amassed over more than 30 years, on the population dynamics of 8 primate species at Ngogo in Uganda provide one of the most detailed accounts to date of changes in a primate community over time. Chapman and coworkers<sup>34</sup> have provided another detailed study of long-term primate population and community dynamics. Using a novel, spatially explicit approach, Willems and Hill<sup>35</sup> simultaneously quantified how the

### Box 1. Glossary

**Community composition** - the species found in a community and their abundances.

**Community ecology** - "The ecology of sets of coexisting species interacting at local scales."<sup>25</sup>

**Co-occurrence patterns** - patterns based on the presence or absence of species across sites that have been argued to reflect community assembly rules (for example, checkerboard distribution).<sup>136</sup>

**Correspondence analysis** - a multivariate analysis that uses multiple independent variables to predict multiple dependent variables while accounting for covariation among variables. It is also an ordination technique that reduces the dimensionality of data so that it can be displayed on a two-dimensional plot in which the proximity of points indicates similarity; the predictor variables driving this similarity are also visualized.

**Dispersal limitation** - "the failure of species to reach all sites

favorable for their growth and survival."<sup>137</sup>

**Macroecology** - the study, by examining statistical relationships, of the patterns and processes driving the abundance and distribution of species over large spatial and temporal scales.<sup>27</sup>

**Mantel test** - a type of analysis in which two or more matrices of pairwise distance measures (for example, genetic, phylogenetic, ecological, or geographic) are compared by creating a null model with permutations. The test produces a significance value ( $p$ ) for the correlation between matrices ( $r$ ).<sup>138</sup>

**Metacommunity** - a set of local communities connected through the dispersal of many potentially interacting species.<sup>139</sup>

**Nestedness** - a pattern that occurs when species in smaller fragments contain (nested) subsets of the species found in more species-rich areas.<sup>140</sup>

**Null model analysis** - "A pattern generating model that is based on randomization of ecological data or random sampling from a known or imagined distribution."<sup>141</sup>

**Path analysis** - a tool for presenting outputs from multiple linear regression that allows for examination of both direct and indirect effects as well as correlations between explanatory variables.

**Phylogeography** - study of the historical and phylogenetic aspects of the spatial distributions of genealogical lineages, especially of closely related species.<sup>142</sup>

**Phylogenetics** - the study of the evolutionary relationships among groups of organisms

**Vicariance** - "The emergence of geographic barriers to dispersal and gene flow, which spatially isolates populations and may lead to the formation of new species through allopatric speciation."<sup>143</sup>

perceived risk of various predators and resource distribution affects vervet ranging behavior. Importantly, vervets respond differently to members of their predator community (leopards, baboons, snakes, eagles); their interactions with some, but not all predators can outweigh the effects of local resources on ranging behavior. Studies of the feeding preferences of predators in a community context have suggested that predation is likely contingent on prey availability. In Tai National Park, Cote d'Ivoire, predation rates vary between predator taxa based on the body size and habitat use of prey species.<sup>36</sup> More specifically, predators favor terrestrial prey with large bodies and small brains that live in small groups, but those preferences vary across predators.<sup>37</sup> Thus, examining the broader predator community may be necessary to understand a species' anti-predator behavior.

Research focused on interspecific competition among primates, as well as primates and other vertebrates,

has progressed during the last several years. It is notoriously difficult to provide evidence of interspecific competition, especially in the absence of experimental data.<sup>38</sup> Nevertheless, studies using novel datasets and quantitative approaches have suggested that primate communities have been shaped by interspecific competition between primate species, as well as between primates and other taxa. At the local scale, body size is important in competitive interactions between species. For example, body size determines dominance hierarchies among species and predicts contest competition in four sympatric primates in Kibale forest (chimpanzees, red-tailed monkeys, blue monkeys, and gray-cheeked mangabeys).<sup>39</sup> Irrespective of taxon, body size significantly predicted competitive outcomes in an observational study of 19 frugivorous vertebrate species (4 primates, 2 squirrels, 13 birds) in feeding trees in a Central African forest.<sup>40</sup> Among the frugivores in Gunung Palung

National Park, Indonesia, gibbons have the highest dietary overlap with squirrels, primates, and hornbills, which highlights the potential role of interspecific competition between primate and nonprimate taxa at the local scale.<sup>41</sup>

### Primate Communities at the Macro Scale

Macroecological studies examine relationships between species and their environment over large spatial and long temporal scales based on the idea that local-scale processes cannot entirely explain species distributions.<sup>27</sup> Several studies have examined various aspects of primate communities at the macro-scale. This work has expanded on prior research in several directions, including investigating the importance of current environmental conditions and historical patterns of dispersal and vicariance.<sup>42-45</sup> Macroecological studies of primates have yielded several interesting and sometimes

unexpected findings. For instance, in many cases the best predictor of how similar the species composition of two communities will be is the distance between them.<sup>42,43</sup> Within a continent, communities in close proximity to each other have similar species compositions, and this similarity decreases as the geographic distance increases. This geographic distance effect may be a surrogate for historical patterns of species dispersal and vicariance. As distance between sites increases, the likelihood that barriers inhibiting dispersal and driving allopatric speciation occur also increases. These barriers do not affect all species equally. Recent evidence suggests that certain biological traits, such as body size or ecological specialization, may influence a species' ability to cross river barriers.<sup>46</sup> However, a recent analysis of Neotropical primate communities suggests that, independent of historical effects such as riverine barriers and Pleistocene refugia, geographic distance effects alone explain the greatest variation in community composition.<sup>47</sup>

Environmental variables are often relatively weak predictors of primate community structure,<sup>42,43,47</sup> which suggests that many primate species are ecologically flexible. Indeed, primate community similarity was weakly and not significantly predicted by tree community similarity in a study of protected areas across Uganda,<sup>48</sup> explicitly demonstrating that primate community composition at these sites does not respond significantly to geographical variation in plant food sources. One interpretation is that these studies collectively provide support for the neutral theory of biodiversity and biogeography.<sup>49</sup> This is the idea that species distributions are largely the result of neutral processes, such as dispersal limitation, and that ecological influences are less important. However, neutral theory is based on the assumption that all species are functionally equivalent. An alternative interpretation of these results is that quantifying important variation in functional traits across taxa may inform our understanding of why primate communities appear to be strongly affected by neutral processes.

Of course, even if elements of the neutral theory of biodiversity and biogeography are supported by some research, this does not negate numerous studies showing important connections between climate, habitat, and various aspects of primate community ecology and macroecology. Since Reed and Bidner's review,<sup>19</sup> additional papers have addressed habitat and resource effects on primate communities. The spatial scale of these studies has ranged from micro-habitat use<sup>50</sup> to the effects of flooded and unflooded adjacent forests on primate use,<sup>51</sup> to regional scale differences in primate community structure,<sup>52</sup> variation in primate communities across ecoregions,<sup>44</sup> and global scale relationships between vegetation and community structure.<sup>53</sup> Across habitats in Madagascar, the protein-to-fiber ratio of leaves predicts lemur biomass<sup>54</sup>; across regions excluding Madagascar, fruit fall predicts primate diversity,<sup>55</sup> and frugivore biomass increases with annual fruit fall and decreases with seasonality.<sup>56</sup>

A macro-level perspective has also been implemented to examine the influence of predators on the interspecific interactions among primates in communities. Terborgh<sup>57</sup> first suggested that variation in primate predators across regions could explain primate polyspecific associations. Specifically, he argued that the strong influence of raptor predation in Africa and the Neotropics explained the frequently observed polyspecific associations of primates in these regions. Similarly, Terborgh suggested that the lack of raptor predation in Madagascar and Asia explained the absence of polyspecific associations in those regions. However, Hart<sup>58</sup> performed a continental comparison of more than 2,200 successful predations on primates: finding that raptors were responsible for most predations in Madagascar. This observation has been confirmed by detailed field investigations in Madagascar. Karpanty<sup>59</sup> found that high predation rates by two diurnal raptors were likely responsible for reducing population growth rates and the carrying capacity of several lemur species at Ranomafana National Park.

Terborgh's argument that primate polyspecific associations are limited to biogeographical regions in which raptors heavily prey on primates may still have applicability, despite heavy raptor predation on Madagascar. Recently published findings show that some lemurs do form polyspecific associations.<sup>60,61</sup> There is, however, a distinction between predation risk,<sup>62</sup> which might drive polyspecific associations, and the number of predation events, which Hart reports. Furthermore, biogeographical differences in predation risk and predation rates will depend on both predator assemblages (above and beyond the presence or absence of raptors) and the prey assemblages at a particular site.

Broad-scale approaches that have been increasingly used to examine interspecific competition among primates and other species have yielded interesting results. Schreier and coworkers<sup>63</sup> examined primate communities in 43 forests globally to quantify potentially competing pairs of species (defined as sympatric species with similar body sizes and dietary preferences) and describe niche separation within those pairs. Variation in forest type, canopy use, and diet were the most common forms of niche separation between potentially competing species pairs.

Null-model analysis of co-occurrence patterns indicate that, in most regions of the world, frugivorous primates are less likely to coexist than are species occupying different dietary niches.<sup>64</sup> Interspecific competition for fruit may therefore be stronger than competition for other food types, and may prevent some frugivorous primates from co-existing in the same community within regions. Interestingly, this is not the case for primates of the Sunda Shelf. In comparable analyses of Bornean communities, Beaudrot and colleagues<sup>65,66</sup> found patterns consistent with the interpretation that while frugivorous primate species did co-occur in the same communities, competition with birds, bats, and squirrels was more severe, potentially leading to competitive exclusion between certain primates and nonprimate vertebrates. Evidence of competitive exclusion was strongest between

## Box 2. Online Resources for Data and Data Analysis

### Resources for data

WorldClim - <http://worldclim.org/>  
 Global Climate Models - <http://www.ccafs-climate.org/>  
 Intergovernmental Panel on Climate Change - <http://www.ipcc-data.org/>  
 Center for International Earth Science Information Network - [http://www.ciesin.columbia.edu/download\\_data.html](http://www.ciesin.columbia.edu/download_data.html)  
 USGS Land Cover Institute - <http://landcover.usgs.gov/landcoverdata.php/>  
 Gridded Population of the World - <http://sedac.ciesin.columbia.edu/gpw/>  
 Human Footprint - [http://ciesin.columbia.edu/wild\\_areas/](http://ciesin.columbia.edu/wild_areas/)  
 Ecological Data Wiki - <http://www.ecologicaldata.org/>  
 Harmonized World Soil Database - <http://www.iiasa.ac.at/Research/LUC/External-World-soil-database/HTML/>  
 Ecological Society of America Data Registry - <http://data.esa.org/esa/style/skins/esa/index.jsp>  
 Global Biodiversity Information Facility - <http://www.gbif.org/>  
 IUCN Red List of Threatened Species Spatial Data - <http://www.iucnredlist.org/technical-documents/spatial-data>  
 Biological Inventories of the World's Protected Areas - <http://www.ice.ucdavis.edu/bioinventory/bioinventory.html>  
 Map of Life - <http://www.mappinglife.org/>  
 Protected Planet - <http://protectedplanet.net/>  
 All the World's Primates - <http://www.alltheworldsprimates.org>

### Resources for data analysis

vegan: Community Ecology Package - <http://cran.r-project.org/web/packages/vegan/index.html>  
 Picante: R tools for integrating phylogenies and ecology - <http://picante.r-forge.r-project.org/>  
 Spatial Analysis in Macroecology - <http://www.ecoevol.ufg.br/sam/>  
 Nestedness Temperature Calculator Program - <http://aics-research.com/nestedness/tempcalc.html>  
 ANINHADO (Nestedness software) - <http://www.guimaraes.bio.br/soft.html>  
 Ecosim - <http://www.uvm.edu/~ngotelli/EcoSim/EcoSim.html>  
 EstimateS - <http://viceroy.eeb.uconn.edu/estimates/index.html>  
 MaxENT - <http://www.cs.princeton.edu/~schapire/maxent/>  
 Canoco (Canonical Ordination) - <http://www.pri.wur.nl/uk/products/canoco/>  
 BioGeoSim - <http://garyentsminger.com/biogeosim/index.htm>  
 OpenGeoDa - <https://geodacenter.asu.edu/projects/opengeoda>  
 GRASS GIS - <http://grass.fbk.eu/>  
 Calendar of Spatial Analysis Training Courses in R - [http://spatial-analyst.net/wiki/index.php?title=Training\\_in\\_R](http://spatial-analyst.net/wiki/index.php?title=Training_in_R)

invertebrate-eating primates and other taxa, especially birds and squirrels. These results support Ganzhorn's hypothesis that Asian primates compete less among themselves than they do with other taxa.<sup>67</sup> Extreme fluctuations in food availability characteristic of Southeast Asian forests<sup>68</sup> may make it necessary for fruit-eaters to fall back on alternative food sources when fruit is scarce, essentially causing them to become generalists.

Interspecific competition among primates has also been examined using a phylogenetic approach. Kamilar and Guidi<sup>69</sup> found that

Malagasy primate communities are less likely than other regions to contain many closely related species. If closely related species occupy similar ecological niches, then this pattern may indicate that past competition structured many Malagasy primate communities. Another reason for this finding may be the large proportion of Malagasy primate species that have become extinct in the recent past, though a recent study suggests that this is not the primary cause of phylogenetically distinct species comprising modern Malagasy communities.<sup>70</sup> Rather, the

phylogenetic structure of Madagascar's primate communities may be the result of the rapid diversification that likely occurred early in lemur history. Given that primates dominate the terrestrial mammalian fauna on Madagascar, competition between primate species may be more severe on Madagascar than in other regions.<sup>43,67</sup>

Research on primate disease ecology has expanded extensively during the last ten years<sup>71</sup> and some recent work has examined this topic in the context of primate communities.<sup>72</sup> Given the close evolutionary

relationship between humans and nonhuman primates, primate disease ecology is highly relevant to understanding aspects of human health. It is also important for conservation, given the significant impact diseases can have on population dynamics. Some major findings include that protozoan parasite species richness increases towards the tropics, but the species richness of viruses and helminthes does not.<sup>73</sup> This has potentially important implications for primate community ecology, since the most species-rich and diverse primate communities are exposed to more protozoan parasites. Phylogenetic studies have shown that parasites are shared most often between closely related species with overlapping geographic ranges<sup>74</sup> and that most primate parasites are generalists. Also, although there is little evidence of host-switching, there is evidence of co-evolution of parasites and their hosts.<sup>75</sup> Variation in primate community size and diversity may therefore be associated with starkly different parasites, which may affect the long-term health of primate species in different types of communities.

There is also a positive relationship between the intensity of range use and parasite richness.<sup>76</sup> During times of scarcity of preferred foods, primates may reduce their daily travel distance or more intensely use areas with available food resources.<sup>77,78</sup> If interspecific competition reduces the availability of preferred food sources, then it may indirectly contribute to increased parasite richness via increased intensity of range use. A more extensive review of primate disease ecology is available elsewhere.<sup>71</sup>

#### WHERE CAN WE GO FROM HERE?

While the past decade has included progress in our understanding of primate community ecology, several major areas remain undeveloped and warrant greater attention in the coming years. A more synthetic study of primate communities is now possible and will undoubtedly lead to important insights. For

instance, it is now possible to examine the distribution and co-existence of primate species in the context of current and past ecological parameters, anthropogenic effects, phylogenetic structure, interactions with nonprimate vertebrates, and the biological traits of the primates themselves. Numerous publicly available databases contain information about a wide array of primate traits, including many aspects of their biogeography, behavior, ecology, and

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phylogeny. Future studies will be facilitated by the continued availability of these data and the implementation of new quantitative techniques (Box 2). Primatologists can play a key role in contributing to and using online data repositories to enhance collaboration and synthetic analysis. In addition, primate ecologists can further enhance their “analytical toolbox” by improving their skills in GIS and spatial analysis, phylogenetic comparative methods, and macroecological modeling. There are short-

term workshops focused on ecological and evolutionary methods available to both graduate students and faculty, including the Bodega Applied Phylogenetics Workshop ([http://bodegaphylo.wikispot.org/Front\\_Page](http://bodegaphylo.wikispot.org/Front_Page)), and the Anthrotree Workshop (<http://www.anthrotreeworkshop.info/>). Combining this wealth of information with new analytical tools will facilitate addressing novel questions or classic questions in new ways (Box 3).

New developments in field-based hardware are beginning to provide detailed data on interspecific interactions. Advances in radio-collar technologies have led to the ability to track multiple species simultaneously, as has been done on Barro Colorado Island, where researchers have used an automated telemetry system for remote study of 38 sympatric animal species, including 17 mammal and 12 bird species.<sup>79</sup> This system, which makes it possible to simultaneously track difficult-to-follow elusive predators and their prey thereby has the potential ability to revolutionize the study of predator-prey interactions.<sup>80</sup> In other cases, increased implementation of camera traps has resulted in a better understanding of tropical mammal community structure and diversity,<sup>81,82</sup> and the shared habitat use of difficult-to-habituate species.<sup>83,84</sup> Gathering more detailed information about primate predators and competitors will provide a more complete picture of community dynamics.

In addition to technological advances, applying conceptual frameworks developed for other taxonomic groups may advance our knowledge of primate community ecology. For example, the stress-gradient hypothesis<sup>85</sup> for understanding positive interspecific interactions has received considerable investigation in plant community ecology,<sup>86</sup> but remains relatively unexplored in animal community ecology. Positive interactions between species are those in which one or both species benefit from the interaction and neither species is harmed. The stress-gradient hypothesis posits that positive interactions will occur more often under high stress levels caused either by consumer pressure (such

### Box 3. Examples of Questions That Can Be Addressed Using Currently Available Data and Analytical Methods

1. Is competition stronger between primate species or between primates and nonprimate vertebrates? How does this vary across regions?
2. Are current or past ecological conditions more important for predicting modern primate distributions?
3. How have primate communities changed through time?
4. Do the macroecological patterns of primate communities, such as the importance of geographic distance to explain species composition, hold true at smaller spatial scales?
5. How do anthropogenic effects influence species distributions and the composition of primate communities?
6. Are some primate species more susceptible than others to negative impacts from climate change and, if so, what factors predict this susceptibility?
7. Can we reconstruct the dispersal of human ancestors by examining the paleobiogeography of other vertebrates?
8. Why are many primate species limited in their dispersal ability?

as predation) or physical stress (for example, harsh climate and low food availability). When consumer pressure is high, species are more likely to form associational defenses to reduce consumer pressure. Similarly, when physical stress is high, species interactions that reduce the physical stressor are more likely to occur. In

the absence of high consumer pressure and high physical stress, positive interactions are expected to be rare. Among primates, polyspecific associations perhaps provide the clearest opportunity for positive interspecific interactions (although not all polyspecific associations are necessarily positive). The framework

from the stress-gradient hypothesis may shed light on why primate polyspecific associations occur in some species or forests, but not others,<sup>87,88</sup> given that primate polyspecific associations have been observed to reduce predation pressure<sup>89</sup> in some instances and enhance foraging<sup>90</sup> in others (Fig. 2).

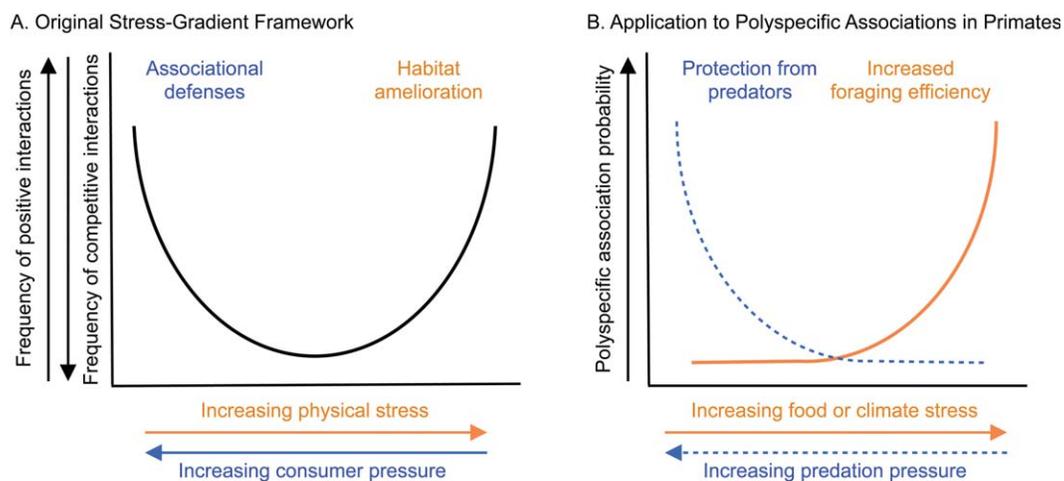


Figure 2. Conceptual framework of the stress-gradient hypothesis. This framework may provide insight into predicting the occurrence of polyspecific associations in primates. A: The stress-gradient hypothesis posits that positive interactions are expected to increase under conditions of high stress. Positive interactions between species are those in which one or both species benefit from the interaction and neither species is harmed. High consumer pressure may result in species forming associations to increase their defenses against predators (that is, associational defenses). High physical or abiotic stress may result in species interacting in ways to decrease physical stress (for example, habitat amelioration). Therefore, if either consumer pressure or physical stress is high, positive interactions among species are expected to be more common and competitive interactions are expected to be rare. B: Among primates, high predation pressure may drive the formation of polyspecific associations to reduce the risk of predation; high stress from harsh climatic conditions or low food availability may drive the formation of polyspecific associations to increase foraging efficiency. In the absence of high predation pressure or stress from food or climate, the probability of a polyspecific association in primates is low. While this framework has received extensive attention in plant community ecology (>700 studies),<sup>86</sup> its applicability to animal communities is relatively untested. Figure modified from original source.<sup>85</sup>

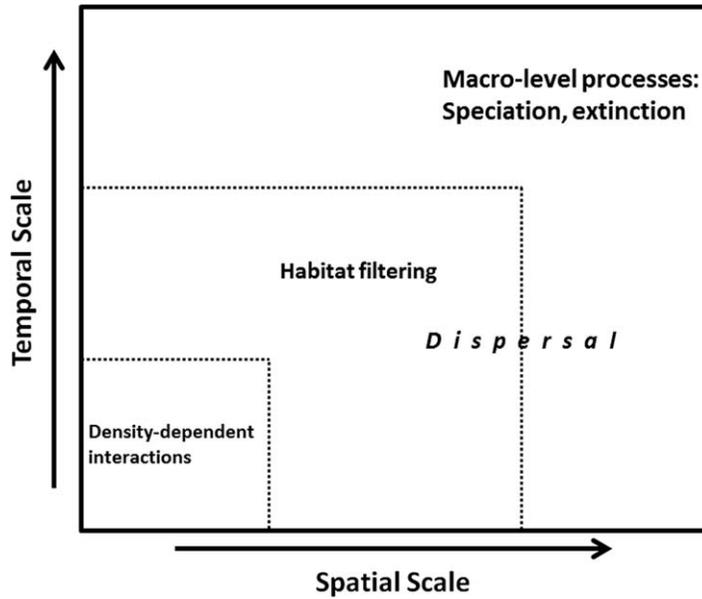


Figure 3. Temporal and spatial scaling in community ecology and evolution. Species distributions and, therefore, community compositions, are driven by biogeographic factors such as speciation and extinction process at large spatial and temporal scales. The importance of dispersal, which varies with the mobility of species, can influence species distributions that are based primarily on ecological factors. At moderate scales, environmental factors filter out species that are intolerant to local conditions. These environmental factors may include abiotic variables such as temperature and rainfall or biotic variables such as predator abundance or prey availability. At fine spatial and temporal scales, density-dependent effects are thought to be most important. These effects include competition, pathogen risk, and mutualisms. For a given point in time or space, multiple factors are often responsible for species distributions and the resulting communities.<sup>135</sup> Adapted from Cavender-Bares and coworkers.<sup>135</sup>

Besides primate-primate relationships, investigations focused on primate-plant interactions have the potential to provide a greater understanding of the maintenance of tropical biodiversity. For example, it is well documented that some primate species destroy seeds through seed predation,<sup>91–94</sup> yet the consequences of this seed predation remain largely understudied. Among nonprimate taxa, scientists have demonstrated not only that variation in terrestrial mammal community composition affects plant community composition through post-dispersal seed predation,<sup>95</sup> but that seed predators contribute to the diversity of Neotropical plant communities because they disproportionately feed on common seeds. This provides a survival advantage to the seeds of rare species.<sup>96</sup> Some primates likely perform similarly important ecological functions through predispersal seed predation. Thus, the community level effects of predispersal seed predation

by primates warrant consideration in future studies, particularly with regard to predicting cascading effects following the extirpation of primates.<sup>97</sup>

A major area of research that remains to be explored is the spatial and temporal scaling of the processes affecting community composition, such as dispersal (Fig. 3). For example, field observations provide data on individual primates dispersing from their natal groups at relatively fine spatial and temporal scales. Molecular, morphological, and phylogenetic data provide information on large-scale patterns of species dispersal across regions and continents.<sup>98–101</sup> Nevertheless, we have little knowledge of how small-scale processes, such as individual dispersal, translate into large-scale patterns of macroecology and community structure over many generations. > For example, how do individual dispersal events result in population- and species-level range patterns at larger

geographic scales? This is one line of research that may begin to link processes at multiple scales. In addition, investigating the role of sociality on species-level dispersal limitation may shed light on why primate species limit their dispersal. Research on translocations, which can be considered “forced dispersal” experiments, has shown that maintenance of family groups is important for individual survival and reproduction rates.<sup>102</sup> If group living imposes greater dispersal costs on individuals than does solitary living, then group-living species would be expected to exhibit greater dispersal limitation than do solitary species. Territoriality is also likely to play a major role in limiting dispersal success because individuals may encounter high rates of aggression from territorial conspecifics.<sup>102</sup> Therefore, investigating the relationship between social structure and dispersal limitation may provide another promising line of future research that links processes at multiple scales.

Because of the feasibility of primate habituation, as well as the painstaking efforts of dawn to dusk behavioral field work, many primatologists have tremendous individual-level data that are essentially unattainable for other animal taxa, particularly in the tropics. Consequently, primatologists are uniquely situated to harness this understanding of individuals to inform studies of population-, community-, and ecosystem-level processes. Connecting individual variation across ecological scales is a burgeoning area of research. Recent reviews have provided conceptual models aimed at integrating data from disparate sources to provide an understanding of the evolutionary ecology of individual differences.<sup>103,104</sup>

Scaling has received more attention in the context of genetic data and its importance for inferring phylogenetic relationships. Because of the relatively manageable number of primate species and the extensive efforts devoted to primate genome sequencing, primate phylogenies are relatively well-resolved in comparison with those of other taxa, especially other tropical organisms. Studies of primate phylogenetics

stand to contribute meaningfully to the field of macroecology. Prominent studies have recently used the well-resolved nature of primate phylogeny to inform our understanding of macroevolutionary processes.<sup>105–107</sup>

Research in phylogeography, which explicitly examines phylogeny in a spatial and biogeographic context, can contribute to our understanding of the historical processes shaping the current distributions of closely related taxa.<sup>98,108</sup> For instance, a study of mouse lemur phylogeography<sup>109</sup> found that monophyletic clades (based on mitochondrial DNA) are distributed in north/south groups, as opposed to an expected east/west division. This finding and additional research nicely illustrate that the commonly held assumptions about the nature of biogeographic patterns may need to be reevaluated when molecular data are integrated into biogeography and macroecology research.

Future work on primate communities can also have important implications for primate conservation. Comparative studies of primate communities can highlight taxa of conservation concern by identifying biological traits associated with increased extinction risk.<sup>17,110</sup> Macroecological and phylogenetic studies can help identify species that are more sensitive to environmental conditions and anthropogenic effects, such as the increased impact of logging on phylogenetically older species,<sup>111</sup> and species for which efforts should be prioritized to conserve phylogenetic diversity.<sup>112</sup> Understanding primate interactions with the broader suite of vertebrates with which they co-occur has potential implications for long-term conservation strategies, such as translocations, which may become more common for establishing, reestablishing, or augmenting populations of threatened species. For example, a review of more than 90 translocated vertebrate species found that translocations into areas with potential competitors were less successful than translocations into areas without competitors or congeners.<sup>113</sup> In addition, the recent development of spatial tools for modeling the effects of hunting on populations and communities has the potential to assist

conservation prioritization.<sup>114</sup> Spatial analyses may also be important for understanding forest fragmentation effects on primate community structure. Increasing forest fragmentation results in the presence of more edge habitats (transitional areas between forest and nonforest habitat), which are known to differently affect primate population densities.<sup>115</sup> Focusing research on primate communities in these areas may contribute to maintaining viable primate populations, as well as understanding the relationship between primates and forest structure.

Research addressing primate paleocommunities can uncover temporal shifts in community structure, especially in relation to climate change and anthropogenic effects on community composition.<sup>70</sup> Integrating data on past and present primate communities can provide insights into temporal changes in community size, composition, phylogenetic structure, and aspects of community niche space. Using historical species distributions can help us understand how species ranges will shift in response to climate change. As human influences on landscapes increase and anthropogenic climate change restructures ecological communities, integrative methods that incorporate data related to extant and extinct species, as well as other approaches, such as ecological niche modeling,<sup>116–119</sup> will become increasingly important as predictive tools for conservation planning.

### APPLYING COMMUNITY ECOLOGY APPROACHES TO OTHER TOPICS IN BIOLOGICAL ANTHROPOLOGY

Community ecology and macroecological approaches can be applied to related fields of study to address questions of interest to biological anthropologists. In fact, a recent paper by Anemone and colleagues<sup>120</sup> stressed the use of GIS and macroecological modeling techniques to predict new fossil localities. This approach is similar to predicting previously unknown occurrences of extant species using known localities

from museum collections and field surveys, is combined with GIS data layers that capture abiotic variables such as temperature, rainfall, and elevation.<sup>121,122</sup> Understanding the biogeographic and community-level patterns of extant primates can provide an important starting point for examining extinct human and nonhuman primate distributions.

Another critical area of research that may benefit from a community ecology approach is reconstructing past environments. In particular, understanding the ecological context of fossil hominins can provide important insights into many aspects of their biology, including diet, locomotion, and predators. One method of paleoenvironmental reconstruction focuses on using the presence or absence of large mammal fossil assemblages.<sup>123–126</sup> Many species are significantly correlated to certain habitat types and can therefore be used to identify historical environments. For instance, a species-rich mammal paleocommunity comprised of many grazers, such as *Alcelaphus*, would indicate a relatively open habitat with significant grassland. If a fossil hominin species were found in this habitat, it would likely be interpreted as being more bipedal than arboreal.

Methods and recent results drawn from studies focused on broad-scale patterns in primate community variation may be able to provide new directions for paleoecological research. Although some paleoecological studies use numerous sites to examine the relationship between species assemblages and ecology, few have attempted quantitative investigation of how the degree of interconnectivity among sites influences mammal paleocommunity structure. Analyses of extant primate communities have found that in many cases the best predictor of community composition is not the local ecology, but the distance to neighboring communities.<sup>42,43</sup> Applying a similar approach to mammal paleocommunities may provide information regarding the dispersal patterns of these taxa, including those of fossil hominin species. This would build on recent publications focused on hominin dispersal routes within and between

continents<sup>100,127,128</sup> that implemented more descriptive approaches.

Finally, methods and theory typically used to understand broad-scale patterns in primate communities can be applied to cultural data. In recent years, anthropologists interested in the evolution of human and nonhuman primate culture have adapted phylogenetic methods.<sup>129–131</sup> Similarly, methods often used in community ecology research, such as Mantel tests and canonical correspondence analyses, can be applied to cultural questions. For instance, they can be used to test the importance of environmental factors and geographic distance for predicting the presence and absence of cultural traits across multiple sites.<sup>132–134</sup> Studies of human and chimpanzee cultural variation have shown that sites in close proximity to each other exhibit similar cultural assemblages and that this similarity decreases with increasing geographic distance. In contrast, local ecological factors poorly predict cultural similarity among sites at broad spatial scales. Applying additional community ecology methods may hold promise for increasing our understanding of broad-scale geographic variation in cultural repertoires.

## CONCLUSIONS

There have been many developments in primate community ecology and macroecology during the past ten years, particularly on the topics of predation, interspecific competition, habitat associations, polyspecific associations, and disease ecology, and much of the research is relevant to conservation. This work has benefitted from newly available data, better organization of existing data, and advances in analytical methods. Although the progress in primate community ecology and macroecology is impressive, there still are numerous directions that can be pursued in the future. We have highlighted some unanswered research questions and drawn attention to relevant theoretical frameworks, analytical tools, and publicly available databases. There are many opportunities for biological

anthropologists to engage in the study of primate communities and contribute to the theoretical and applied areas described here, as well as others. We hope that in the future more primate researchers will address community- and macro-level ecological questions.

## ACKNOWLEDGMENTS

JMK thanks John Fleagle, Charlie Janson, and Kaye Reed; LB thanks Andy Marshall and Sandy Harcourt for insightful conversations about primate community ecology and biogeography. LB also thanks Marcel Rejmánek, Sharon Lawler, and Marcel Holyoak for discussions about community ecology in other systems. Four anonymous reviewers and John Fleagle provided helpful comments that improved earlier versions of this manuscript.

## REFERENCES

- Fleagle JG, Janson CH, Reed KE, editors. 1999. Primate communities. New York: Cambridge University Press.
- Blackburn TM, Gaston KJ. 2003. Macroecology: concepts and consequences. Malden, MA: Blackwell Science.
- Gaston KJ. 2000. Pattern and process in macroecology. Malden, MA, Blackwell Science.
- Harte J. 2011. Maximum entropy and ecology: a theory of abundance, distribution, and energetics. New York: Oxford University Press.
- Corlett RT, Primack RB. 2006. Tropical rainforests and the need for cross-continental comparisons. *Trends Ecol Evol* 21:104–110.
- Emmons LH. 1999. Of mice and monkeys: primates as predictors of mammal community richness. In: Fleagle JG, Janson C, Reed KE, editors. Primate communities. Cambridge: Cambridge University Press. p 171–188.
- Lawes MJ, Eeley AC. 2000. Are local patterns of anthropoid primate diversity related to patterns of diversity at a larger scale? *J Biogeogr* 27:1421–1425.
- Harcourt AH. 2006. Rarity in the tropics: biogeography and macroecology of the primates. *J Biogeogr* 33:2077–2087.
- Fleagle JG, Lehman SM, editors. 2006. Primate biogeography: progress and prospects. New York: Springer.
- Conroy GC. 2003. The inverse relationship between species diversity and body mass: do primates play by the "rules"? *J Hum Evol* 45: 43–55.
- Harcourt AH, Schreier BM. 2009. Diversity, body mass, and latitudinal gradients in primates. *Int J Primatol* 30:283–300.
- Doherty DA, Harcourt AH. 2004. Are rare primate taxa specialists or simply less studied? *J Biogeogr* 31:57–61.
- Harcourt AH, Coppeto SA, Parks SA. 2005. The distribution-abundance (i.e. density) relationship: its form and causes in a tropical mammal order, Primates. *J Biogeogr* 32:565–579.
- Harcourt AH. 2000. Latitude and latitudinal extent: a global analysis of the Rapoport effect in a tropical mammalian taxon: Primates. *J Biogeogr* 27:1169–1182.
- Reed KE, Fleagle JG. 1995. Geographic and climatic control of primate diversity. *Proc Natl Acad Sci USA* 92:7874–7876.
- Fleagle JG, Reed KE. 1996. Comparing primate communities: a multivariate approach. *J Hum Evol* 30:489–510.
- Jernvall J, Wright PC. 1998. Diversity components of impending primate extinctions. *Proc Natl Acad Sci USA* 95:11279–11283.
- Kay RF, Madden RH, van Schaik CP, et al. 1997. Primate species richness is determined by plant productivity: implications for conservation. *Proc Natl Acad Sci USA* 94:13023–13027.
- Reed KE, Bidner LR. 2004. Primate communities: past, present and possible future. *Yearbk Phys Anthropol* 47:2–39.
- Ganzhorn JU, Arrigo-Nelson S, Boinski S, et al. 2009. Possible fruit protein effects on primate communities in Madagascar and the Neotropics. *PLoS ONE* 4:e8253.
- Lehman SM. 2000. Primate community structure in Guyana: A biogeographical analysis. *Int J Primatol* 21:489–510.
- Lehman SM. 2004. Distribution and diversity of primates in Guyana: Species-area relationships and riverine barriers. *Int J Primatol* 25:73–95.
- Chapman CA, Balcomb SR, Gillespie TR, et al. 2000. Long-term effects of logging on African primate communities: a 28-year comparison from Kibale National Park, Uganda. *Conserv Biol* 14:207–217.
- Peres CA, Dolman PM. 2000. Density compensation in Neotropical primate communities: evidence from 56 hunted and nonhunted Amazonian forests of varying productivity. *Oecologia* 122:175–189.
- Lawton JH. 1999. Are there general laws in ecology? *Oikos* 84:177–192.
- Terborgh J. 1983. Five New World primates: a study in comparative ecology. Princeton: Princeton University Press.
- Keith SA, Webb TJ, Bohning-Gaese K, et al. 2012. What is macroecology? *Biol Lett* 8:904–906.
- Chapman CA, Onderdonk DA. 1998. Forests without primates: primate/plant codependency. *Am J Primatol* 45:127–141.
- Stevenson PR. 2011. The abundance of large ateline monkeys is positively associated with the diversity of plants regenerating in Neotropical forests. *Biotropica* 43:512–519.
- Nunez-Iturri G, Olsson O, Howe HF. 2008. Hunting reduces recruitment of primate-dispersed trees in Amazonian Peru. *Biol Conserv* 141:1536–1546.
- Vanthomme H, Belle B, Forget PM. 2010. Bushmeat hunting alters recruitment of large-seeded plant species in central Africa. *Biotropica* 42:672–679.
- Poulsen JR, Clark CJ, Bolker BM. 2012. Experimental manipulation of seed shadows of an Afrotropical tree determines drivers of recruitment. *Ecology* 93:500–510.
- Lwanga JS, Struhsaker TT, Struhsaker PJ, et al. 2011. Primate population dynamics over 32.9 years at Ngogo, Kibale National Park, Uganda. *Am J Primatol* 73:997–1011.
- Chapman CA, Struhsaker TT, Skorupa JP, et al. 2010. Understanding long-term primate

community dynamics: implications of forest change. *Ecol Appl* 20:179–191.

35 Willems EP, Hill RA. 2009. Predator-specific landscapes of fear and resource distribution: effects on spatial range use. *Ecology* 90:546–555.

36 Shultz S, Noe R, McGraw WS, et al. 2004. A community-level evaluation of the impact of prey behavioral and ecological characteristics on predator diet composition. *Proc R Soc B* 271: 725–732.

37 Shultz S, Finlayson LV. 2010. Large body and small brain and group sizes are associated with predator preferences for mammalian prey. *Behav Ecol* 21:1073–1079.

38 Connell JH. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35:131–138.

39 Houle A, Chapman CA, Vickery WL. 2010. Intra-tree vertical variation of fruit density and the nature of contest competition in frugivores. *Behav Ecol Sociobiol* 64:429–441.

40 French AR, Smith TB. 2005. Importance of body size in determining dominance hierarchies among diverse tropical frugivores. *Biotropica* 37:96–101.

41 Marshall AJ, Cannon CH, Leighton M. 2009. Competition and niche overlap between gibbons (*Hylobates albobarbis*) and other frugivorous vertebrates in Gunung Palung National Park, West Kalimantan, Indonesia. In: Lappan S, Whittaker DJ, editors. *The gibbons: new perspectives on small ape socioecology and population biology*. Chicago: University of Chicago Press. p 161–188.

42 Kamilar JM. 2009. Environmental and geographic correlates of the taxonomic structure of primate communities. *Am J Phys Anthropol* 139:382–393.

43 Beaudrot L, Marshall AJ. 2011. Primate communities are structured more by dispersal limitation than by niches. *J Anim Ecol* 80:332–341.

44 Muldoon KM, Goodman SM. 2010. Ecological biogeography of Malagasy non-volant mammals: community structure is correlated with habitat. *J Biogeogr* 37:1144–1159.

45 Goodman SM, Ganzhorn JU. 2004. Biogeography of lemurs in the humid forests of Madagascar: the role of elevational distribution and rivers. *J Biogeogr* 31:47–55.

46 Harcourt AH, Wood MA. 2012. Rivers as barriers to primate distributions in Africa. *Int J Primatol* 33:168–183.

47 Gavilanez MM, Stevens RD. 2012. Role of environmental, historical and spatial processes in the structure of Neotropical primate communities: contrasting taxonomic and phylogenetic perspectives. *Global Ecol Biogeogr* 22: 607–619.

48 Beaudrot L, Rejmanek M, Marshall AJ. 2013. Dispersal modes affect tropical forest assembly across trophic levels. *Ecography*.

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

50 Sheth SN, Loiselle BA, Blake JG. 2009. Phylogenetic constraints on fine-scale patterns of habitat use by eight primate species in eastern Ecuador. *J Trop Ecol* 25:571–582.

51 Haugaasen T, Peres CA. 2005. Primate assemblage structure in Amazonian flooded and unflooded forests. *Am J Primatol* 67: 243–258.

52 Palminteri S, Powell GVN, Peres CA. 2011. Regional-scale heterogeneity in primate community structure at multiple undisturbed forest sites across south-eastern Peru. *J Trop Ecol* 27 181–194.

53 Louys J, Meloro C, Elton S, et al. 2011. Mammal community structure correlates with arboreal heterogeneity in faunally and geographically diverse habitats: implications for community convergence. *Global Ecol Biogeogr* 20:717–729.

54 Simmen B, Tamaud L, Hladik A. 2012. Leaf nutritional quality as a predictor of primate biomass: further evidence of an ecological anomaly within prosimian communities in Madagascar. *J Trop Ecol* 28:141–151.

55 Hanya G, Aiba S. 2010. Fruit fall in tropical and temperate forests: implications for frugivore diversity. *Ecol Res* 25:1081–1090.

56 Hanya G, Stevenson P, van Noordwijk M, et al. 2011. Seasonality in fruit availability affects frugivorous primate biomass and species richness. *Ecography* 34:1009–1017.

57 Terborgh J. 1990. Mixed flocks and polyspecific associations: costs and benefits of mixed groups to birds and monkeys. *Am J Primatol* 21:87–100.

58 Hart D. 2007. Predation on primates: a biogeographical analysis. In: Gursky SL, Nekaris KAI, editors. *Primate anti-predator strategies*. New York: Springer Science.

59 Karpanty SM. 2006. Direct and indirect impacts of raptor predation on lemurs in southeastern Madagascar. *Int J Primatol* 27: 239–261.

60 Sauter ML. 2002. Group size effects on predation sensitive foraging in wild ring-tailed lemurs (*Lemur catta*). In: Miller LE, editor. *Eat or be eaten: predator sensitive foraging among primates*. Cambridge: Cambridge University Press. p 107–125.

61 Freed BZ. 2007. Polyspecific associations of crowned lemurs and Sanford's lemurs in Madagascar. In: Gould L, Sauter ML, editors. *Lemurs: ecology and adaptation. Developments in Primatology: Progress and Prospects*. New York: Springer. p 111–131.

62 Janson C. 2003. Puzzles, predation, and primates: using life history to understand selection pressures. In: Kappeler PM, Pereira ME, editors. *Primate life histories and socioecology*. Chicago: University of Chicago Press. p 103–131.

63 Schreier BM, Harcourt AH, Coppeto SA, et al. 2009. Interspecific competition and niche separation in primates: a global analysis. *Biotropica* 41:283–291.

64 Kamilar JM, Ledogar JA. 2011. Species co-occurrence patterns and dietary resource competition in primates. *Am J Phys Anthropol* 144: 131–139.

65 Beaudrot L, Struebig MJ, Meijaard E, et al. 2013. Interspecific interactions between primates, birds, bats and squirrels may affect community composition on Borneo. *Am J Primatol* 75:170–185.

66 Beaudrot L, Struebig MJ, Meijaard E, et al. n.d. Co-occurrence patterns of Bornean vertebrates suggest competitive exclusion is strongest in distantly related taxa. *Oecologia*. In press.

67 Ganzhorn JU. 1999. Body mass, competition and the structure of primate communities. In: Fleagle JG, Janson C, Reed KE, editors. *Primate communities*. Cambridge: Cambridge University Press. p 141–157.

68 Cannon CH, Curran LM, Marshall AJ, et al. 2007. Long-term reproductive behavior of woody plants across seven Bornean forest types in the Gunung Palung National Park, Indonesia: suprannual synchrony, temporal productivity, and fruiting diversity. *Ecol Lett* 10:956–969.

69 Kamilar JM, Guidi LM. 2010. The phylogenetic structure of primate communities: variation within and across continents. *J Biogeogr* 37:801–813.

70 Razafindratsima OH, Mehtani S, Dunham AE. 2012. Extinctions, traits and phylogenetic community structure: insights from primate assemblages in Madagascar. *Ecography* 35:1–10.

71 Nunn CL. 2012. Primate disease ecology in comparative and theoretical perspective. *Am J Primatol* 74:497–509.

72 Altizer S, Nunn CL, Thrall PH, et al. 2003. Social organization and parasite risk in mammals: integrating theory and empirical studies. *Annu Rev Ecol Evol S* 34:517–547.

73 Nunn CL, Altizer SM, Sechrest W, et al. 2005. Latitudinal gradients of parasite species richness in primates. *Divers Distrib* 11:249–256.

74 Davies TJ, Pedersen AB. 2008. Phylogeny and geography predict pathogen community similarity in wild primates and humans. *Proc R Soc B* 275:1695–1701.

75 Cooper N, Griffin R, Franz M, et al. 2012. Phylogenetic host specificity and understanding parasite sharing in primates. *Ecol Lett*. 15: 1370–1377.

76 Nunn CL, Dokey ATW. 2006. Ranging patterns and parasitism in primates. *Biol Lett* 2: 351–354.

77 Marshall AJ, Wrangham RW. 2007. Evolutionary consequences of fallback foods. *Int J Primatol* 28:1219–1235.

78 Hemingway CA, Bynum N. 2005. The influence of seasonality on primate diet and ranging. In: Brockman DK, van Schaik CP, editors. *Seasonality in primates*. Cambridge: Cambridge University Press. p 57–104.

79 Kays R, Tilak S, Crofoot M, et al. 2011. Tracking animal location and activity with an automated radio telemetry system in a tropical rainforest. *Comput J* 54:1931–1948.

80 Aliaga-Rossel E, Moreno RS, Kays RW, et al. 2006. Ocelot (*Leopardus pardalis*) predation on agouti (*Dasyprocta punctata*). *Biotropica* 38:691–694.

81 Ahumada JA, Silva CEF, Gajapersad K, et al. 2011. Community structure and diversity of tropical forest mammals: data from a global camera trap network. *Philos Trans Royal Soc B* 366:2703–2711.

82 Gerber B, Karpanty SM, Crawford C, et al. 2010. An assessment of carnivore relative abundance and density in the eastern rainforests of Madagascar using remotely triggered camera traps. *Oryx* 44:219–222.

83 Bowkett AE, Rovero F, Marshall AR. 2008. The use of camera-trap data to model habitat use by antelope species in the Udzungwa mountain forests, Tanzania. *Afr J Ecol* 46:479–487.

84 Russak SM. 2013. Shifting the focus in primate community ecology: utilizing patch focals to study unhabituated dry habitat chimpanzees. *Am J Phys Anthropol* 150:237.

85 Bertness MD, Callaway R. 1994. Positive interactions in communities. *Trends Ecol Evol* 9: 191–193.

86 He Q, Bertness MD, Altieri AH. 2013. Global shifts towards positive species interactions with increasing environmental stress. *Ecol Lett*. 16: 695–706.

87 Haugaasen T, Peres CA. 2009. Interspecific primate associations in Amazonian flooded and unflooded forests. *Primates* 50:239–251.

- 88 Lehman SM. 2000. Primate community structure in Guyana: A biogeographic analysis. *Int J Primatol* 21:333–351.
- 89 Buzzard PJ. 2010. Polyspecific associations of *Cercopithecus campbelli* and *C. petaurista* with *C. diana*: What are the costs and benefits? *Primates* 51:307–314.
- 90 Porter LM. 2001. Benefits of polyspecific associations for the Goeldi's monkey (*Callimico goeldii*). *Am J Primatol* 54:143–158.
- 91 Peres CA. 1991. Seed predation of *Cariniana micrantha* (Lecythidaceae) by brown capuchin monkeys in central Amazonia. *Biotropica* 23:262–270.
- 92 Davies G. 1991. Seed-eating by red leaf monkeys (*Presbytis rubicunda*) in dipterocarp forest of northern Borneo. *Int J Primatol* 12:119–144.
- 93 Bowler M, Bodmer RE. 2011. Diet and food choice in Peruvian red uakaris (*Cacajao calvus ucayalii*): Selective or opportunistic seed predation? *Int J Primatol* 32:1109–1122.
- 94 Koyabu DB, Endo H. 2010. Craniodental mechanics and diet in Asian colobines: morphological evidence of mature seed predation and sclerocarpy. *Am J Phys Anthropol* 142:137–148.
- 95 Asquith NM, Wright SJ, Clausen MJ. 1997. Does mammal community composition control recruitment in Neotropical forests? Evidence from Panama. *Ecology* 78:941–946.
- 96 Paine CET, Beck H. 2007. Seed predation by Neotropical rainforest mammals increases diversity in seedling recruitment. *Ecology* 88:3076–3087.
- 97 Stoner KE, Riba-Hernandez P, Vulinec K, et al. 2007. The role of mammals in creating and modifying seedshadows in tropical forests and some possible consequences of their elimination. *Biotropica* 39:316–327.
- 98 Chan LM, Brown JL, Yoder AD. 2011. Integrating statistical genetic and geospatial methods brings new power to phylogeography. *Mol Phylogen Evol* 59:523–537.
- 99 McGraw WS, Fleagle JG. 2006. Biogeography and evolution of the *Cercocebus-Mandrillus* clade: evidence from the face. In: Lehman SM, Fleagle JG, editors. *Primate biogeography*. New York: Springer. Pp.201–224.
- 100 Harcourt AH. 2012. *Human biogeography*. Berkeley: University of California Press.
- 101 Kamilar JM, Martin SK, Tosi AJ. 2009. Combining biogeographic and phylogenetic data to examine primate speciation: an example using guenon monkeys. *Biotropica* 41:514–519.
- 102 Swaisgood RR. 2010. The conservation-welfare nexus in reintroduction programmes: a role for sensory ecology. *Anim Welfare* 19:125–137.
- 103 Bolnick DI, Amarasekare P, Araujo MS, et al. 2011. Why intraspecific trait variation matters in community ecology. *Trends Ecol Evol* 26:183–192.
- 104 Dall SR, Bell AM, Bolnick DI, et al. 2012. An evolutionary ecology of individual differences. *Ecol Lett* 15:1189–1198.
- 105 Shultz S, Opie C, Atkinson QD. 2011. Step-wise evolution of stable sociality in primates. *Nature* 479:219–222.
- 106 Magnuson-Ford K, Otto SP. 2012. Linking the investigations of character evolution and species diversification. *Am Nat* 180:225–245.
- 107 Kamilar JM, Cooper N. 2013. Phylogenetic signal in primate behavior, ecology and life history. *Philos Trans Royal Soc B* 368:20120341.
- 108 Pastorini J, Thalmann U, Martin RD. 2003. A molecular approach to comparative phylogeography of extant Malagasy lemurs. *Proc Natl Acad Sci USA* 100:5879–5884.
- 109 Yoder AD, Heckman K. 2006. Mouse lemur phylogeography revises a model of ecogeographic constraint in Madagascar. In: Lehman SM, Fleagle JG, editors. *Primate biogeography: Progress and prospects*. New York: Springer. p 255–268.
- 110 Cardillo M, Mace GM, Jones KE, et al. 2005. Multiple causes of high extinction risk in large mammal species. *Science* 309:1239–1241.
- 111 Meijaard E, Sheil D, Marshall AJ, et al. 2008. Phylogenetic diversity is positively correlated with sensitivity to timber harvest in Bornean mammals. *Biotropica* 40:76–85.
- 112 McGoogan K, Kivell T, Hutchison M, et al. 2007. Phylogenetic diversity and the conservation biogeography of African primates. *J Biogeogr* 34:1962–1974.
- 113 Griffith B, Scott JM, Carpenter JW, et al. 1989. Translocation as a species conservation tool: status and strategy. *Science* 245:477–480.
- 114 Levi T, Shepard GH, Ohi-Schacherer J, et al. 2011. Spatial tools for modeling the sustainability of subsistence hunting in tropical forests. *Ecol Appl* 21:1802–1818.
- 115 Lehman SM, Rajaonson A, Day S. 2006. Edge effects and their influence on lemur density and distribution in southeast Madagascar. *Am J Phys Anthropol* 129:232–241.
- 116 Vidal-Garcia F, Serio-Silva JC. 2011. Potential distribution of Mexican primates: modeling the ecological niche with the maximum entropy algorithm. *Primates* 52:261–270.
- 117 Boublil J, de Lima MG. 2009. Modeling the geographical distribution and fundamental niches of *Cacajao* spp. and *Chiropotes israelita* in northwestern Amazonia via a maximum entropy algorithm. *Int J Primatol* 30:217–228.
- 118 Thorn JS, Nijman V, Smith D, et al. 2009. Ecological niche modelling as a technique for assessing threats and setting conservation priorities for Asian slow lorises (Primates: Nycticebus). *Divers Distrib* 15:289–298.
- 119 Kamilar JM, Muldoon KM. 2010. The climatic niche diversity of Malagasy primates: a phylogenetic approach. *PLoS ONE* 5: e11073. doi:10.1371/journal.pone.0011073.
- 120 Anemone RL, Conroy GC, Emerson CW. 2011. GIS and paleoanthropology: incorporating new approaches from the geospatial sciences in the analysis of primate and human evolution. *Am J Phys Anthropol* 146:19–46.
- 121 Graham CH, Ferrier S, Huettman F, et al. 2004. New developments in museum-based informatics and applications in biodiversity analysis. *Trends Ecol Evol* 19:497–503.
- 122 Phillips SJ, Dudik M. 2008. Modeling of species distributions with maxent: new extensions and a comprehensive evaluation. *Ecography* 31:161–175.
- 123 Reed KE. 1998. Using large mammal communities to examine ecological and taxonomic structure and predict vegetation in extant and extinct assemblages. *Paleobiology* 24:384–408.
- 124 Reed KE. 2008. Paleocological patterns at the Hadar hominin site, Afar regional state, Ethiopia. *J Hum Evol* 54:743–768.
- 125 Plummer TW, Bishop LC. 1994. Hominid paleoecology at Olduvai Gorge, Tanzania as indicated by antelope remains. *J Hum Evol* 27:47–75.
- 126 Bobe R, Behrensmeyer AK, Chapman RE. 2002. Faunal change, environmental variability and late Pliocene hominin evolution. *J Hum Evol* 42:475–497.
- 127 O'Regan HJ, Turner A, Bishop LC, et al. 2011. Hominins without fellow travellers? First appearances and inferred dispersals of Afro-Eurasian large mammals in the Plio-Pleistocene. *Quaternary Sci Rev* 30: 1343–1352.
- 128 Fleagle JG, Shea JJ, Grine FE, Baden AL, editors. 2010. *Out of Africa I: the first hominin colonization of Eurasia*. New York: Springer.
- 129 Lycett SJ, Collard M, McGrew WC. 2009. Cladistic analyses of behavioural variation in wild *Pan troglodytes*: exploring the chimpanzee culture hypothesis. *J Hum Evol* 57:337–349.
- 130 Walker RS, Wichmann S, Mailund T, et al. 2012. Cultural phylogenetics of the Tupi language family in lowland South America. *Plos One* 7.
- 131 Matthews LJ, Tehrani JJ, Jordan FM, et al. 2011. Testing for divergent transmission histories among cultural characters: a study using Bayesian phylogenetic methods and Iranian tribal textile data. *Plos One* 6.
- 132 Jordan P, Shennan S. 2003. Cultural transmission, language, and basketry traditions amongst the California Indians. *J Anthropol Archaeol* 22:42–74.
- 133 Kamilar JM, Marshack JL. 2012. Does geography or ecology best explain “cultural” variation among chimpanzee communities? *J Hum Evol* 62:256–260.
- 134 van Schaik CP, Ancrenaz M, Borgen G, et al. 2003. Orangutan cultures and the evolution of material culture. *Science* 299:102–105.
- 135 Cavender-Bares J, Kozak K, Fine P, Kembel S. 2009. The merging of community ecology and phylogenetic biology. *Ecol Letters* 12:693–715.
- 136 Gotelli NJ. 2000. Null model analysis of species co-occurrence patterns. *Ecology* 81:2606–2621.
- 137 Hubbell SP. 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. *Funct Ecol* 19:166–172.
- 138 Smouse PE, Long JC, Sokal RR. 1986. Multiple regression and correlation extensions of the Mantel test of matrix correspondence. *Syst Zool* 35:627–632.
- 139 Leibold MA, Holyoak M, Mouquet N, et al. 2004. The metacommunity concept: a framework for multiscale community ecology. *Ecol Lett* 7:601–613.
- 140 Atmar W, Patterson BD. 1993. The measure of order and disorder in the distribution of fragmented habitat. *Oecologia* 96:373–382.
- 141 Gotelli NJ, Graves GR. 1996. *Null models in ecology*. Washington D.C.: Smithsonian Institution Press.
- 142 Avise JC. 2000. *Phylogeography: the history and formation of species*. Cambridge: Harvard University Press.
- 143 Albert JS, Crampton WG. 2010. The geography and ecology of diversification in Neotropical freshwaters. *Nat Edu Knowledge* 3:13.