

1 Community Ecology of the Middle Miocene Primates of La Venta,  
2 Colombia: the Relationship between Ecological Diversity, Divergence  
3 Time, and Phylogenetic Richness

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27 **Abstract**

28 It has been suggested that the degree of ecological diversity that characterizes a primate  
29 community correlates positively with both its phylogenetic richness  
30 and the time since the members of that community diverged (Fleagle and Reed 1999). It is  
31 therefore questionable whether or not a community with a relatively recent divergence time  
32 but high phylogenetic richness would be as ecologically variable as a community with  
33 similar phylogenetic richness but a more distant divergence time. To address this question,  
34 the ecological diversity of a fossil primate community from La Venta, Colombia, a Middle  
35 Miocene platyrrhine community with phylogenetic diversity comparable to extant  
36 platyrrhine communities but a relatively short time since divergence, was compared with  
37 that of modern neotropical primate communities. Shearing quotients and molar lengths,  
38 which together are reliable indicators of diet, for both fossil and extant species were plotted  
39 against each other to describe the dietary “ecospace” occupied by each community.  
40 Community diversity was calculated as the area of the minimum convex polygon  
41 encompassing all community members. The diversity of the fossil community was then  
42 compared to that of extant communities to test if the fossil community was less diverse  
43 than extant communities while taking phylogenetic richness into account. Results indicate  
44 that the La Ventan community was not significantly less ecologically diverse than modern  
45 communities, supporting the idea that ecological diversification occurred along with  
46 phylogenetic diversification early in platyrrhine evolution.

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48 Key words: New World monkeys; Ecospace; Primate communities; Dietary diversity;  
49 Primate evolution

50

51 **Introduction**

52

53           Studies of primate communities over the past decade have used multivariate “ecospace”  
54 to describe the ecological diversity that characterizes a given community (e.g., Fleagle and Reed  
55 1996; Godfrey et al. 1997; Gilbert 2005; see also Novack-Gottshall 2007). A community’s  
56 ecospace can be defined as the space it takes up on multivariate axes which represent a variety of  
57 ecological variables (including diet, locomotor and positional behavior, activity pattern, and  
58 body size) and describe the niche of each species present in the community (see Fleagle and  
59 Reed 1996). Such analyses have demonstrated a positive relationship between the ecological  
60 diversity of a primate community and the degree of phylogenetic richness in that community  
61 (Fleagle and Reed 1999). Similarly, primate communities whose members share a more ancient  
62 common ancestor tend to be more diverse than those communities whose members share a more  
63 recent ancestor (Fleagle and Reed 1999). Specifically, Neotropical primate communities, whose  
64 members diverged relatively recently (20 Ma) (Hodgson et al. 2009), are much less ecologically  
65 diverse than Old World primate communities (Fleagle and Reed 1999), whose members share a  
66 more ancient common ancestor (80-90 Ma for African and Asian communities: Eizirik et al.  
67 2004; 40 to 65 Ma for the Malagasy communities: Yoder and Yang 2004).

68           To date, studies correlating ecological diversity in primate communities with either  
69 phylogenetic diversity or time since divergence have not compared the ecological variation of  
70 fossil primate communities with that of living communities. Such a comparison is especially apt  
71 when examining the affect divergence time has on platyrrhine communities because there is little  
72 variation in average time since divergence among most New World primate communities due to  
73 the fact that most modern subfamilies appeared relatively early in platyrrhine evolution

74 (Rosenberger et al. 2009). The fossil community from La Venta, **Colombia** (see Fleagle et al.  
75 1997) demonstrates a degree of phylogenetic richness (i.e., number of taxa) comparable to  
76 modern communities (Rosenberger et al. 2009), with many taxa attributable to extant subfamilies  
77 (Fig. 1), yet with a time since divergence roughly one third that of modern platyrrhines. The  
78 positive relationship between ecological diversity and divergence time of primate communities  
79 (Fleagle and Reed 1999) predicts that the fossil primate community at La Venta would be less  
80 ecologically diverse than modern platyrrhine communities. However, because the phylogenetic  
81 richness of the primate community from La Venta is comparable to many modern platyrrhine  
82 communities, it is questionable whether the degree of diversity of the La Ventan primates would  
83 be less than that of modern primate communities with a similar degree of phylogenetic diversity,  
84 despite their shorter divergence time.

85         This study addresses this question by first examining how phylogenetic richness affects  
86 ecological diversity (as determined by variation in dental measurements related to diet and body  
87 size) in modern neotropical communities. The degree of ecological diversity of the La Ventan  
88 fauna is then compared to that of the modern communities while taking the number of taxa  
89 present in the community into account. It was predicted that modern communities with greater  
90 phylogenetic richness would be more ecologically variable than less rich communities, and that  
91 the La Ventan community would be less ecologically diverse than modern communities given its  
92 degree of phylogenetic richness. This comparison of the La Ventan fossil community to modern  
93 communities provides insight into whether ecological diversity has remained relatively static  
94 since the divergence of the major extant platyrrhine clades, or if ecological diversity continued to  
95 increase even after the initial adaptive radiation.

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## Methods

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Diversity in the dietary ecology of the Middle Miocene fossil primate community at La Venta (see Kay and Madden 1997 for details regarding the paleoecology of La Venta) is here compared to that of nine modern neotropical primate communities (fig. 2, table 1). Extant communities were chosen such that a range of degrees phylogenetic diversity would be represented (see table 1 for a list of all species present at each site). The fossil community was limited to the **five primate** species associated with the La Ventan “Monkey Beds” sedimentary deposits (including ***Aotus dindensis***, *Cebupithecia sarmientoi*, *Mohanamico hershkovitzi*, *Neosaimiri fieldsi*, and *Stirtonia tatacoensis*) (Fleagle et al., 1997; Hartwig and Meldrum, 2002) **plus the one species found in deposits both above and below the Monkey Beds (*Patasola magdalenae*)**. *Micodon kiotensis* is also associated with the Monkey Beds but was not included as a member of the fossil community because the limited fossil remains of this genus do not allow for detailed analysis regarding its ecology (Rosenberger et al. 2009) and the specimens ascribed to this genus may actually be deciduous teeth of another La Ventan primate species such as *Neosaimiri* (Fleagle et al. 1997; Fleagle pers. comm.). The Monkey Beds date to slightly less than 13 Ma (Madden et al. 1997; **Flynn et al. 1997; but see Takemura et al. 1992 for slightly older dates for younger La Ventan deposits**) and are thought to represent a short enough period of time (approximately 15 ky; Kay and Madden 1997) that it is likely that the species found in this deposit co-existed.

Ecological diversity was determined through analysis of variation in shearing quotients (SQ) and length of the lower first molar ( $M_1$ ), which respectively are indicative of diet (Kay 1975) and body size (Gingerich et al. 1982). Shearing quotients are a measure of the development of the molar shearing crests; low (negative) SQ values indicate rounded molar

121 cusps and are associated with largely frugivorous diets while high (positive) values indicate  
122 high-crested molars and are associated with largely folivorous (at large body sizes) or  
123 insectivorous (at small body sizes) diets (see Kay 1975; Ungar and Kay 1995). These  
124 measurements have been published for both fossil and extant taxa (Anthony and Kay 1993;  
125 Fleagle et al. 1997; Meldrum and Kay 1997; Currie Ketchum 2002) and are perhaps the only  
126 diet-related variables that are measurable for all species concerned, given that some fossil taxa  
127 are represented exclusively by dental remains. Measurements are species averages (see table 2  
128 for values of all measurements used) and were not measured for the specific populations used in  
129 this study.

130 The M<sub>1</sub> length and SQ for each species were plotted against each other on a bivariate plot  
131 to determine the dietary “ecospace” occupied by each primate assemblage (fig. 3). Following  
132 Fleagle and Reed (1996), ecological diversity for each community was calculated as the area of  
133 the minimum convex polygon (MCP) that encompasses the position of all species of that  
134 community on the bivariate plot. MCPs were made from bivariate scatter plots made in  
135 Microsoft Excel. The scale of each plot was standardized (as in fig. 3) so that the MCP area for  
136 each community was directly comparable to those of all other communities. MCP areas were  
137 calculated by importing each plot into Adobe Illustrator 12.0, dividing each MCP into multiple  
138 triangles, and summing the areas of all constituting triangles. One mm of M1 length was given a  
139 value of 3.175 cm in Adobe Illustrator, while 10 SQ units were given a value of 2.25 cm

140 Phylogenetic diversity for each community was measured using three methods: 1) the  
141 number of species, 2) the number of genera, and 3) the number of subfamilies which make up the  
142 community. Traditional (conservative) species designations were used following Fleagle (1999).  
143 Based on Schneider (in Schneider and Rosenberger 1996), the following five subfamilies of

144 extant platyrrhines were recognized for the current study: Callitrichinae, Aotinae, Cebinae,  
145 Atelinae, and Pitheciinae. Some researchers break the Platyrrhini down into additional (smaller)  
146 groups, but only these five subfamilies were used because they are now widely accepted as  
147 natural groupings (reviewed in Rylands et al. 2000; Rylands and Mittermeier 2009). The **six**  
148 **fossil taxa constituting the Miocene community** were considered to be stem or crown members  
149 of these subfamilies (fig. 1). Based on Fleagle and Kay (1997), *Cebupithecia sarmientoi* is  
150 placed within the Pitheciinae and *Patasola magdalenae* is placed with the Callitrichinae. Based  
151 on Rosenberger et al. (2009), ***Aotus dindensis* is placed within the Aotinae**, *Neosaimiri fieldsi* is  
152 placed within the Cebinae, *Stirtonia tatacoensis* is placed within the Atelinae, and *Mohanamico*  
153 *hershkovitzi* is placed within the Callitrichinae. It should be noted that the status of *Mohanamico*  
154 is disputed, with Kay (1990) arguing that it is likely a pithecine. However, whether one places  
155 this species within the callitrichines or the pithecines does not affect the current analysis because  
156 it does not change the number of species, genera, or subfamilies present in the Monkey Beds  
157 community.

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## 159 Statistical Analyses

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161 To examine the relationship between phylogenetic and ecological diversity, a linear  
162 regression was used to test if each of the three measures of phylogenetic richness (i.e., number of  
163 species, genera, and subfamilies) was a significant predictor of ecological diversity in the extant  
164 communities. The area of the MCP of the La Ventan community was then compared to that of  
165 the extant communities, taking into account each measure of phylogenetic richness which was  
166 significant in the regressions. This was tested by measuring the vertical distance to the regression



167 line (i.e., the residual) on the plot of MCP area against phylogenetic richness for each of the  
168 extant communities (fig. 4); a positive value was given to those points above the regression line  
169 and a negative value to those below. The La Ventan community was then superimposed on the  
170 graph (based on its MCP area and phylogenetic richness) and its vertical distance from the  
171 regression line was measured. A special case t-test for comparing a single specimen against a  
172 sample (Sokal and Rohlf 1995) was then used to test if the residual of the La Ventan community  
173 differed significantly from those of the extant communities. Such a method allows for a test of  
174 whether or not the La Ventan community was less diverse while taking phylogenetic richness  
175 into account. Linear regressions were conducted using SPSS 15.0. The special case t-tests were  
176 conducted by hand.

177

## 178 **Results**

179

180 Among extant communities, ecological diversity (as measured by MCP area) varied  
181 considerably (Table 3) and was positively associated with each measure of phylogenetic  
182 richness. Each of the number of species ( $n=9$ ,  $R^2=0.537$ ,  $p=0.025$ ; fig. 5), the number of genera  
183 ( $n=9$ ,  $R^2=0.564$ ,  $p=0.020$ ; fig. 6), and the number of subfamilies ( $n=9$ ,  $R^2=0.597$ ,  $p=0.015$ ; fig. 7)  
184 were significant predictors of the area of the MCPs. When the La Ventan community is  
185 superimposed onto these plots, it consistently falls below the regression line (figs. 5-7).  
186 However, the degree to which the La Ventan community falls below the regression line is not  
187 significantly different from that of the extant communities, regardless of how phylogenetic  
188 richness was measured (number of species:  $t=-0.167$ ,  $df=8$ ,  $p>0.90$ ; number of genera:  $t=-0.463$ ,  
189  $df=8$ ,  $p>0.90$ ; number of subfamilies:  $t=-1.567$ ,  $df=8$ ,  $p>0.10$ ).

190

191 **Discussion**

192

193 As expected, the greatest diversity in dietary ecospace as measured by the area of the  
194 MCP was found in communities with the greatest degree of phylogenetic richness. This  
195 relationship held whether phylogenetic richness was defined as the number of species, number of  
196 genera, or number of subfamilies present in a given community. Differences in ecological  
197 diversity between the La Ventan fossil community and modern communities, however, were not  
198 significant. It thus seems that much of the ecological diversity that characterizes extant  
199 Neotropical primate communities occurred early in the adaptive radiation of modern platyrrhines  
200 (i.e., from 20 to 13 Ma) and that phylogenetic richness explains the degree of ecological diversity  
201 that characterizes platyrrhine communities to a greater extent than does the time elapsed since  
202 the members of that community diverged (see Fleagle and Reed 1999).

203 Despite the lack of a significant difference, it appears that some expansion in dietary  
204 ecospace has occurred among New World primates over the last 13 million years (fig. 8). This  
205 increase is related to both greater diversity in  $M_1$  lengths among extant platyrrhines and a slight  
206 increase in SQs at both small and large body size, with the species of La Venta having lower SQs  
207 than many of their extant relatives. This may be indicative of an increased reliance on insectivory  
208 and folivory in some modern taxa relative to the species of the fossil community. However, Kay  
209 and Ungar (1997) found that although SQs of some Miocene catarrhines were low relative to  
210 their modern relatives, dental microwear indicated that the Miocene fauna were as folivorous as  
211 modern catarrhines with relatively high SQs. The authors argued that this may be an example of  
212 the “Red Queen effect” (see Van Valen 1973), in which these folivorous taxa became better  
213 adapted to the niche they already occupied as a means to compete with other contemporaneous

214 folivores. It is possible that a similar phenomenon occurred in the course of platyrrhine  
215 evolution; studies of microscopic dental wear in these fossil species would provide insight in this  
216 regard. In addition to an increase in SQs, some of the expansion of ecospace that has taken place  
217 over the last 13 million years is the result of a greater diversity of M<sub>1</sub> lengths among extant taxa  
218 relative to the species of the La Ventan Monkey Beds. If relatively recent platyrrhine  
219 communities, such as those which included *Protopithecus* and *Caipora*, were included among  
220 modern communities, the dietary ecospace would be considerably larger, as these taxa are up to  
221 twice the size of any modern New World primate (MacPhee and Horovitz 2002; Rosenberger et  
222 al. 2009).

223 Finally, the lack of a significant difference between La Venta and the extant communities  
224 may be due to a type II error. It is possible that if other fossil platyrrhine communities dating to  
225 the Middle Miocene were available for examination, a significant difference in ecological  
226 diversity between the extinct and extant communities could be found. However, because of the  
227 dearth of known fossil platyrrhine communities, this is not possible to test. Results may also  
228 change if additional discoveries increase the number of taxa known from the Monkey Beds or  
229 what we know about the ecology of the taxa already described. Indeed, a number of additional  
230 taxa, including *Lagonimico*, *Nuciraptor*, *Stirtonia victoriae* (Fleagle et al. 1997), and  
231 *Miocallicebus* (Takai et al. 2001) have been found in other La Ventan deposits and may  
232 eventually be known from the Monkey Beds, although their addition to the fossil community  
233 would not necessarily change the results or conclusion of the current study. Among the species  
234 known from other layers, lower dentition is available for three (*Lagonimico*, *Nuciraptor*,  
235 *Stirtonia victoriae*; Fleagle et al., 1997; Meldrum & Kay 1997. While their addition would  
236 indeed add somewhat to the fossil community's MCP area, this would also add to its

237 phylogenetic richness. Whether or not these species should be considered members of the fossil  
238 community awaits further fossil discoveries.

239

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241

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248

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250

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351

352



353 Table 1. The species present in each of the extant communities examined in this study.

subfamily	species	site								
		1	2	3	4	5	6	7	8	9
Pitheciinae	<i>Cacajao calvus</i>								x	
	<i>Callicebus cupreus</i>									x
	<i>Callicebus moloch</i>							x	x	
	<i>Chiropotes satanas</i>				x		x			
	<i>Pithecia monachus</i>								x	
	<i>Pithecia pithecia</i>				x					
Atelinae	<i>Alouatta belzebul</i>						x			
	<i>Alouatta palliata</i>	x	x							
	<i>Alouatta seniculus</i>			x	x	x		x		x
	<i>Ateles belzebuth</i>			x		x				x
	<i>Ateles geoffroyi</i>	x	x							
	<i>Ateles paniscus</i>				x			x		
	<i>Lagothrix lagothricha</i>								x	x
Cebinae	<i>Cebus albifrons</i>			x				x	x	
	<i>Cebus apella</i>				x	x	x	x		x
	<i>Cebus capucinus</i>	x	x							
	<i>Cebus olivaceus</i>					x				
	<i>Saimiri sciureus</i>				x	x	x	x	x	x
Aotinae	<i>Aotus azarae</i>									
	<i>Aotus trivirgatus</i>		x					x		x
Callitrichinae	<i>Cebuella pygmaea</i>								x	
	<i>Saguinus fuscicollis</i>							x	x	
	<i>Saguinus geoffroyi</i>		x							
	<i>Saguinus imperator</i>							x		
	<i>Saguinus leucopus</i>			x						
	<i>Saguinus midas</i>				x		x			
	<i>Saguinus mystax</i>								x	

354 1. La Selva, Costa Rica: Fishkind & Sussman 1987; 2. Barro Colorado Island, Panama: Glanz  
355 1990; 3. Magdalena Valley, Colombia: Green 1978; 4. Raleighvallen, Suriname: Fleagle and  
356 Reed 1996; 5. Maraca Island, Brazil: Mendes-Pontes 1999; 6. Pucurui River, Brazil: Johns 1986;  
357 7. Cocha Cashu, Peru: Fleagle and Reed 1996; 8. Jenaro Herrera, Peru: Aquino 1978; 9. Tinigua,  
358 Colombia: Stevenson 1996.

359

360 Table 2. Dental measurements used in this study.

Species	M <sub>1</sub> length (mm)	SQ*
<i>Alouatta belzebul</i> <sup>2</sup>	7.3	11.5
<i>Alouatta palliata</i> <sup>1</sup>	6.9	10.8
<i>Alouatta seniculus</i> <sup>2</sup>	7.0	12.7
<i>Aotus azarae</i> <sup>2</sup>	3.1	10.9
<i>Aotus dindensis</i>	3.2	4.7
<i>Aotus trivirgatus</i> <sup>1</sup>	3.1	10.9
<i>Ateles belzebuth</i> <sup>2</sup>	5.0	-1.0
<i>Ateles geoffroyi</i> <sup>1</sup>	5.3	-2.5
<i>Ateles paniscus</i> <sup>2</sup>	5.4	-3.5
<i>Cacajao calvus</i> <sup>2</sup>	4.3	-17.2
<i>Callicebus cupreus</i> <sup>2</sup>	3.2	-4.9
<i>Callicebus moloch</i> <sup>1</sup>	3.2	-4.7
<i>Cebuella pygmaea</i> <sup>1</sup>	1.8	0.9
<i>Cebupithecia sarmientoi</i> <sup>1</sup>	3.5	-19.4
<i>Cebus albifrons</i> <sup>2</sup>	4.5	-7.2
<i>Cebus apella</i> <sup>1</sup>	4.8	-11.3
<i>Cebus capucinus</i> <sup>2</sup>	4.5	-7.7
<i>Cebus olivaceus</i> <sup>2</sup>	4.5	-9.6
<i>Chiropotes satanas</i> <sup>1</sup>	3.6	-15.5
<i>Lagothrix lagotricha</i> <sup>1</sup>	5.5	1.9
<i>Mohanamico hershkovitzi</i> <sup>1</sup>	3.2	-14.6
<i>Neosaimiri fieldsi</i> <sup>1</sup>	2.9	-10.3
<i>Patasola magdalenae</i> <sup>1</sup>	2.5	-7.0
<i>Pithecia monachus</i> <sup>1</sup>	4.0	-6.6
<i>Pithecia pithecia</i> <sup>2</sup>	3.5	-4.5
<i>Saguinus fuscicollis</i> <sup>2</sup>	2.1	-7.0
<i>Saguinus geoffroyi</i> <sup>1</sup>	2.6	-7.9
<i>Saguinus imperator</i> <sup>2</sup>	2.5	-11.0
<i>Saguinus leucops</i> <sup>2</sup>	2.4	-9.3
<i>Saguinus midas</i> <sup>2</sup>	2.3	-9.7
<i>Saguinus mystax</i> <sup>1</sup>	2.5	-11.9
<i>Saimiri sciureus</i> <sup>1</sup>	2.9	6.4

361

362 <sup>1</sup> Data from Fleagle et al. (1997). <sup>2</sup> Data from Currie Ketchum (2002). \*Methods for calculating

363 shearing quotients (SQs) described in Fleagle et al. (1997).

364

365 Table 3. Phylogenetic richness and minimum convex polygon (MCP) areas for each of the nine  
 366 extant and one fossil community examined in this study.

site	# species	# genera	# subfamilies	MCP area
La Selva	3	3	2	0.54
BCI*	5	5	4	12.06
Magdalena	4	4	3	3.99
Raleighvallen	7	7	4	15.42
Maraca Island	5	4	2	9.34
Pucurui River	5	5	4	15.63
Jenerro Herera	9	8	5	12.02
Cocha Cashu	9	7	5	16.82
Tiningua	7	7	4	13.35
La Venta	6	6	5	10.36

367 \* Barro Colorado Island

368 **Figure captions**

369

370 **Figure 1.** Cladistic relationships of the extant platyrrhine subfamilies (based on Hodgson et al.  
371 2009) and the placement of La Ventan taxa within those subfamilies. **A= *Aotus dindensis***; C =  
372 *Cebupithecia*; S = *Stirtonia*; N= *Neosaimiri*; M = *Mohanamico*; P = *Patasola*.

373

374 **Figure 2.** The location of La Venta and the nine extant communities examined in this study. 1.  
375 La Selva, Costa Rica. 2. Barro Colorado Island, Panama. 3. Magdalena Valley, Colombia. 4.  
376 Raleighvallen, Suriname. 5. Maraca Island, Brazil. 6. Pucurui River, Brazil. 7. Cocha Cashu,  
377 Peru. 8. Jenaro Herrera, Peru. 9. Tinigua, Colombia.

378

379 **Figure 3.** An example of the method used to calculate ecological diversity for a given  
380 community. This figure shows the shearing quotients (SQs) plotted against the lengths of the first  
381 molars for the five species found in Barro Colorado, Panama. Ecological diversity was calculated  
382 as the area of the minimum convex polygon encompassing all species of the community (see  
383 Fleagle and Reed 1996).

384

385 **Figure 4.** An example of the method used to test for differences in ecological diversity between  
386 the La Ventan fossil community and the extant communities. The diagonal line is the regression  
387 line based on the equation that describes the relationship between the phylogenetic richness (i.e.,  
388 the number of taxa) of the extant communities and the area their minimum convex polygons.  
389 Vertical lines are the vertical distance (i.e., the residual) of each community from the regression

390 line. The fossil community is superimposed on the graph and is not included in the regression  
391 equation.

392

393 **Figure 5.** The relationship between the number of species at a site and the area of the site's  
394 minimum convex polygon. The La Ventan community is superimposed onto the graph.

395

396 **Figure 6.** The relationship between the number of genera at a site and the area of the site's  
397 minimum convex polygon. The La Ventan community is superimposed onto the graph.

398

399 **Figure 7.** The relationship between the number of subfamilies at a site and the area of the site's  
400 minimum convex polygon. The La Ventan community is superimposed onto the graph.

401

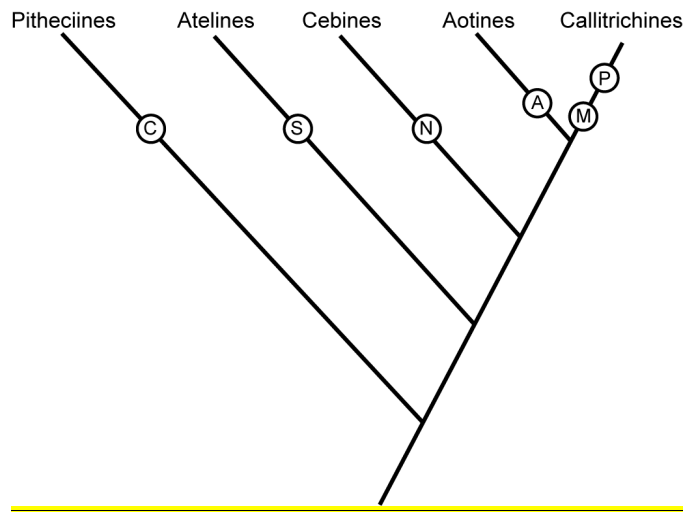
402 **Figure 8.** Scatter plot of shearing quotients (SQs) and M<sub>1</sub> lengths (a proxy for body size) for all  
403 extant and fossil taxa included in the current study. Extant taxa show a greater degree of  
404 variation in SQs at both small and large body size and slightly more variation in M<sub>1</sub> lengths. **A=**

405 ***Aotus dindensis***; C = *Cebupithecia*; S = *Stirtonia*; N= *Neosaimiri*; M = *Mohanamico*; P =  
406 *Patasola*.

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408

409 **Figure 1**



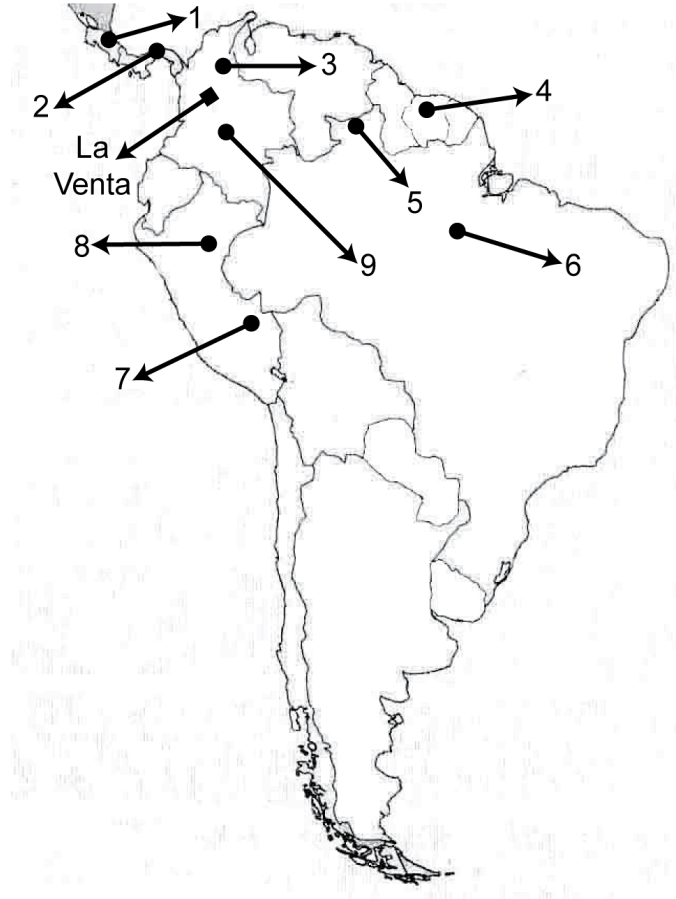
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414 **Figure 2**



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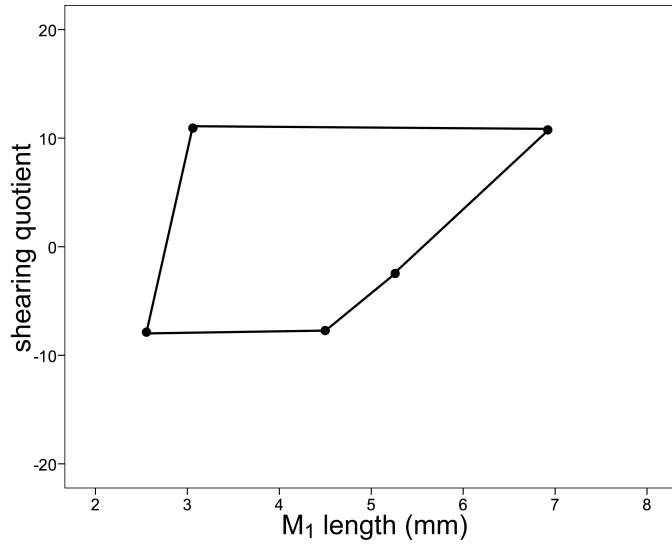
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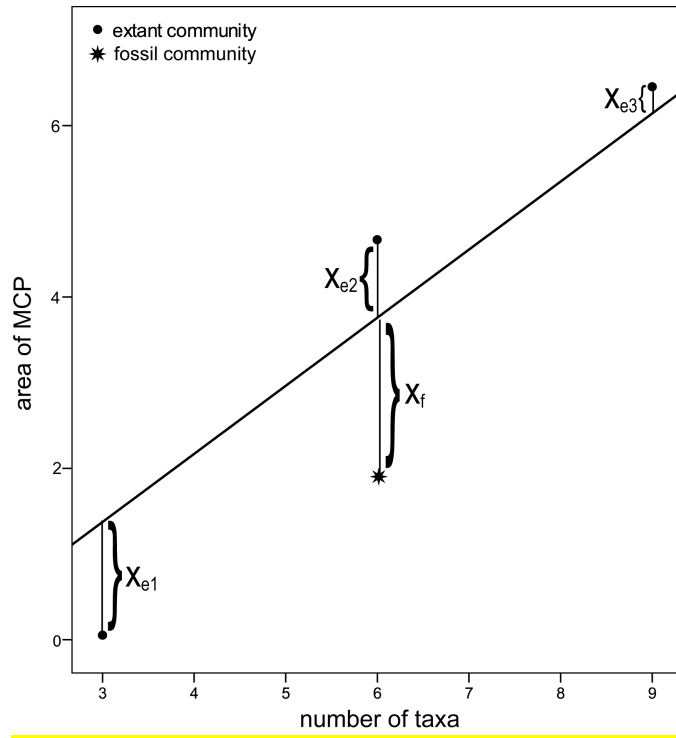
421 **Figure 3**



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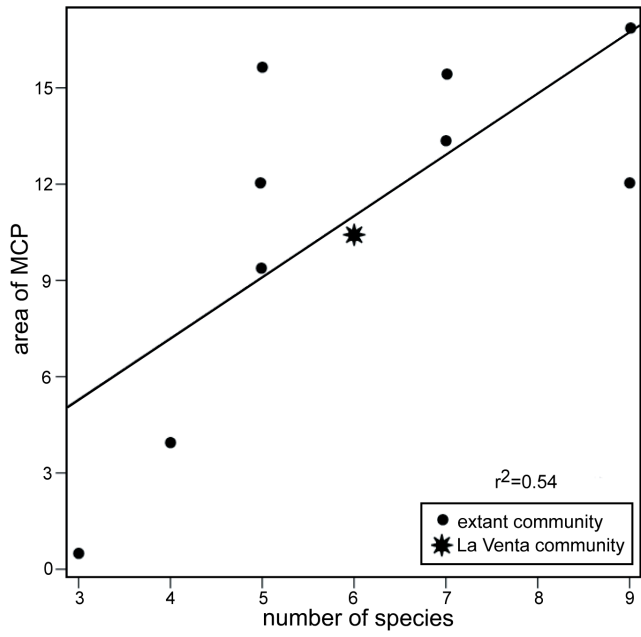


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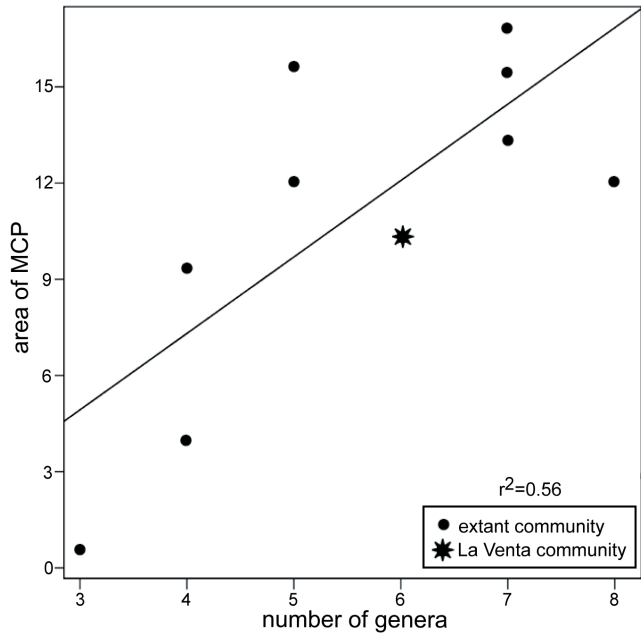
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429 **Figure 5**  
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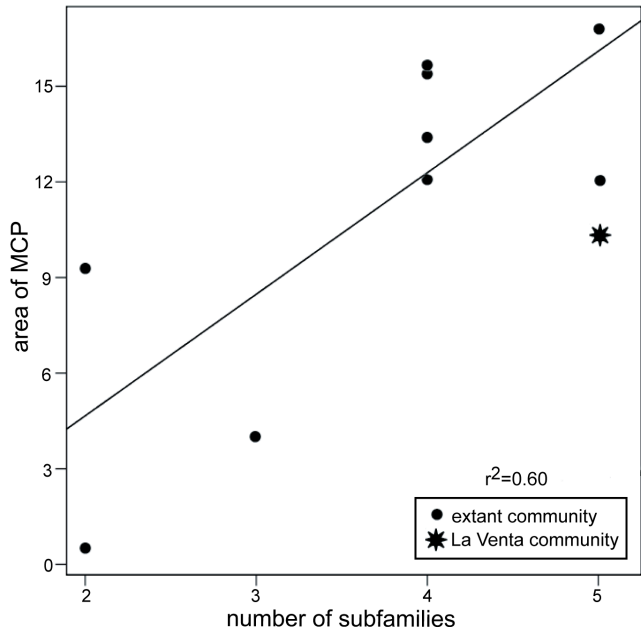
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437 **Figure 6**  
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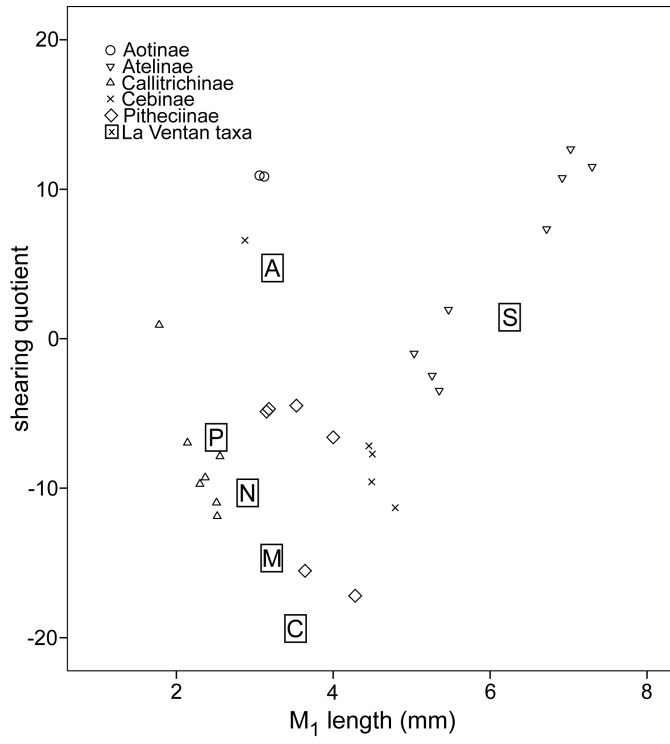
445 **Figure 7**  
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451 **Figure 8**  
452



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