

## Incisor size and community structure in rodents: Two tests of the role of competition

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**Abstract** – We used two different approaches to test for the effect of interspecific competition on community-wide patterns in the size of the upper incisor in six rodent communities. One tests for constancy of size ratios between adjacent species (Barton and David's test), and the other tests for minimum mean size overlap between species pairs (randomization test). The results of the two tests were more congruent for the radius of the upper incisor than for its diameter. Although a number of tests gave significant results, they led to a consistent rejection of the null hypothesis of a randomly generated pattern only in two communities from an African rainforest. Many factors are likely to disturb community structure, among which we identify recent species introductions and the presence of rare species. Our results also show that Hutchinson's rule of a limiting size similarity does not hold; the mean size ratio between adjacent species was correlated with the overall size range and the number of species in a community. © Elsevier, Paris

### Competition / community structure / incisor size / rodents / null models

## 1. INTRODUCTION

The study of the mechanisms that underlie the organization of communities has become one of the fundamental aims of ecology. It involves the analysis of the way that species share food resources, which can be revealed by the size structure of a community. The last twenty years have been marked by many controversies on the nature of this structure and its recognition by statistical methods (see reviews in [8, 17, 28]).

There are some strong relationships between the resources a species utilizes and its morphological characteristics. For instance, Brown [7] showed that for some desert rodents the seed size consumed by a species increases with its body weight. Hutchinson [19] suggested that a minimum size ratio of 1.28 between two species is necessary for their co-occurrence. Brown and Wilson [10] proposed that species in sympatry exert competitive pressures on each other, resulting in a competitive character displacement between them. In a series of recent papers, Dayan and colleagues [11–13] worked on mammal community structure, and showed that the size ratios between three or more sympatric species were more equal than expected by chance alone. They suggested that for het-

eromyid rodents, in which upper incisors are used for seed husking, the ratios for the size of the incisor should be more equal than for other traits such as skull length or body weight [11]. Only dental characters should indeed reveal the size structure of a mammalian community if this structure is due to competition for food.

In order to test this hypothesis, we report similar studies on size differentiation in six rodent communities, ranging from an open environment to a tropical rainforest.

In their study, Dayan and colleagues [11–13] used the method proposed by Barton and David [4] to test for equal size ratios. However, this test is based on a comparison between the mean sizes of a pair of adjacent species, a method which ignores intraspecific variability. If competition occurs, it should be strongest at the extremities of the species' niches, that is, between the largest individuals of the smaller species and the smallest individuals of the larger species. Therefore, we also used a null model approach which takes into account the whole size distribution of each species. The method, which was developed by Loreau [22] to test for temporal niche differentiation in cara-

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bid beetles, tests for minimization of niche overlap between species.

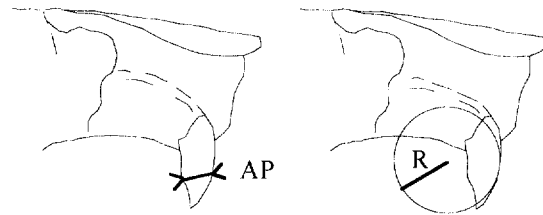
## 2. MATERIALS

The communities studied comprised from four to seven granivorous rodent species and are presented in *table 1*. The assemblages from Makokou (Muridae and Sciuridae) and Azangaro were made up of specimens that were actually living in sympatry. In order to enlarge sample sizes of the three remaining communities (Azrou, Essaouira and Casa Grande), we included specimens that were collected in various locations close to the locality studied. However, this should not influence our results since we checked for the absence of size differences between specimens collected in the locality and the added specimens. The squirrels from Makokou are all arboreal and include in their diet both seeds and fruits. All the other rodent species considered from the five remaining communities are terrestrial, nocturnal and granivore species. Insectivore species and species recently introduced by human agent were not considered in our work. All the specimens were studied at the Museum of Natural History, Paris. We followed the classification proposed by Wilson and Reeder [29] for their taxonomic status.

We chose only adult specimens whose third molar had erupted. We took measurements with a drawing tube coupled with a digitizer to the nearest 0.01 mm for two characters: the antero-posterior diameter (AP) and the radius (R) of the upper incisor (*figure 1*). The incisor radius was computed using four points on the distal edge of the incisor. As intraspecific variability is generally greater than sexual dimorphism for dental measurements in rodents, we did not take the latter into account in this study.

## 3. STATISTICAL METHODS

To test for equality of size ratios, we used Barton and David's ([4] hereafter B&D) statistics [11–13, 26]. This method tests for constancy of ratios between the mean sizes of paired size-ranked species in a community. As in Dayan and Simberloff [11], we used three



**Figure 1.** Anterior part of a rodent skull showing the two measurements taken on the upper incisor: antero-posterior diameter (AP), and radius (R).

B&D statistics:  $G1,n$ , the ratio of the smallest to the largest size ratio;  $G1,n-1$ , the ratio of the smallest to the second largest size ratio; and  $G2,n$ , the ratio of the second smallest to the largest size ratio, which give three probabilities  $P1$ ,  $P2$  and  $P3$ , respectively. The null hypothesis that the observed ratios do not differ from those produced by chance alone is rejected when the probabilities lie under the significance level. To compute these probabilities, we used the original computer program kindly provided to us by D. Simberloff.

We also adapted the method developed by Loreau [22] to our data. This method is based on the principle that competition should minimize size overlap between adjacent species. A randomization procedure allows the species size distributions to shift randomly, and gives the probability of finding an overlap that is smaller than or equal to the observed value. If this probability lies under the significance level, the null hypothesis that the observed overlap is produced by chance alone is rejected. As in Loreau [22], the statistic used was the mean pairwise size overlap between species, where size overlap was calculated following Levins' [21] niche overlap index. As in Loreau [22], the only constraint during the randomization procedure was to maintain the shape of each species' size distribution. Since there are no a priori biological constraints on each species' potential size range, we allowed the species size distributions to shift from that of the smallest species to that of the largest species, throughout the whole size range observed in the com-

**Table 1.** Presentation of the six rodent communities studied. *n*: Number of species.

Community	Location	Description	<i>n</i>
Makokou-Muridae	M'Passa (Gabon)	equatorial evergreen rainforest	6
Makokou-Sciuridae	M'Passa (Gabon)	equatorial evergreen rainforest	7
Essaouira	Haouz plain (Morocco)	semi-arid plain with sandhills	6
Azrou	Middle-Atlas (Morocco)	semi-arid. with shrubs and thornbush species	4
Azangaro	Occidental edge of Andes (Peru)	graminacea steppe	7
Casa Grande	Sonoran desert, Arizona (USA)	desertic sandy soils with mixture of shrub species	5

**Table II.** Means and standard deviations of the antero-posterior diameter (AP) and radius (R) of the upper incisor in mm. Numbers of specimens are in brackets after the species name.

Community	AP	R
<b>Makokou-Muridae</b>		
<i>Hylomyscus parvus</i> (7)	0.96 (0.12)	3.03 (0.33)
<i>H. stella</i> (15)	1.19 (0.12)	2.52 (0.31)
<i>Praomys tulbergi</i> (15)	1.29 (0.25)	2.84 (0.38)
<i>Hybomys univittatus</i> (15)	1.49 (0.14)	3.30 (0.42)
<i>Stochomys longicaudatus</i> (15)	1.96 (0.22)	4.49 (0.63)
<i>Grammomys rutilans</i> (15)	1.54 (0.11)	3.68 (0.57)
<b>Makokou-Sciuridae</b>		
<i>Myosciurus pumilio</i> (1)	1.17 (–)	3.41 (–)
<i>Paraxerus poensis</i> (18)	1.62 (0.25)	4.55 (0.78)
<i>Funisciurus lemniscatus</i> (14)	1.94 (0.16)	4.98 (0.34)
<i>F. pyrrhopus</i> (15)	2.17 (0.23)	6.00 (0.78)
<i>Protoxerus stangeri</i> (8)	3.75 (0.32)	9.48 (1.41)
<i>Heliosciurus rufobrachium</i> (17)	3 (0.38)	7.63 (1.04)
<i>Epixerus ebii</i> (3)	3.84 (0.57)	10.09 (1.73)
<b>Essaouira</b>		
<i>Mus spretus</i> (20)	1.19 (0.07)	2.8 (0.19)
<i>Lemniscomys barbarus</i> (16)	1.64 (0.13)	3.6 (0.5)
<i>Mastomys peregrinus</i> (13)	1.68 (0.15)	3.73 (0.41)
<i>Gerbillus hesperinus</i> (3)	1.87 (0.06)	3.97 (0.26)
<i>G. campestris</i> (20)	1.77 (0.1)	3.85 (0.29)
<i>Meriones shawi</i> (17)	1.82 (0.16)	6.31 (2.09)
<b>Azrou</b>		
<i>Mus spretus</i> (20)	1.19 (0.07)	2.8 (0.19)
<i>Apodemus sylvaticus</i> (20)	1.26 (0.1)	3.05 (0.29)
<i>Gerbillus campestris</i> (20)	1.77 (0.1)	3.85 (0.29)
<i>Meriones shawi</i> (17)	1.82 (0.16)	6.31 (2.09)
<b>Azangaro</b>		
<i>Calomys sorellus</i> (20)	1.16 (0.09)	3.04 (0.2)
<i>C. lepidus</i> (10)	1.04 (0.07)	2.64 (0.22)
<i>Akodon boliviensis</i> (20)	1.15 (0.08)	2.87 (0.28)
<i>A. amoenus</i> (13)	1.07 (0.14)	3.14 (0.62)
<i>Chroeomys jelskii</i> (17)	1.09 (0.08)	3.57 (1.1)
<i>Auliscomys pictus</i> (16)	1.31 (0.19)	3.69 (0.41)
<i>Phyllotis osilae</i> (20)	1.45 (0.08)	3.65 (0.35)
<b>Casa Grande</b>		
<i>Dipodomys merriami</i> (13)	1.53 (0.1)	4.97 (0.38)
<i>D. deserti</i> (1)	1.94 (–)	8.57 (–)
<i>Chaetodipus penicillatus</i> (3)	1.29 (0.01)	3.78 (0.26)
<i>Perognathus longimembris</i> (1)	0.99 (–)	2.98 (–)
<i>Peromyscus maniculatus</i> (6)	1.25 (0.14)	3.14 (0.43)

munity. When the total number of possible arrangements of shifted size distributions exceeded 4 000, only 2 000 arrangements were produced at random.

Otherwise, all the possible arrangements were simulated.

## 4. RESULTS

The mean values of the two characters measured on the upper incisor in the six communities are given in *table II*.

### 4.1. Preliminary results on constraints in the randomization test

#### 4.1.1. Effect of size-scale subdivision

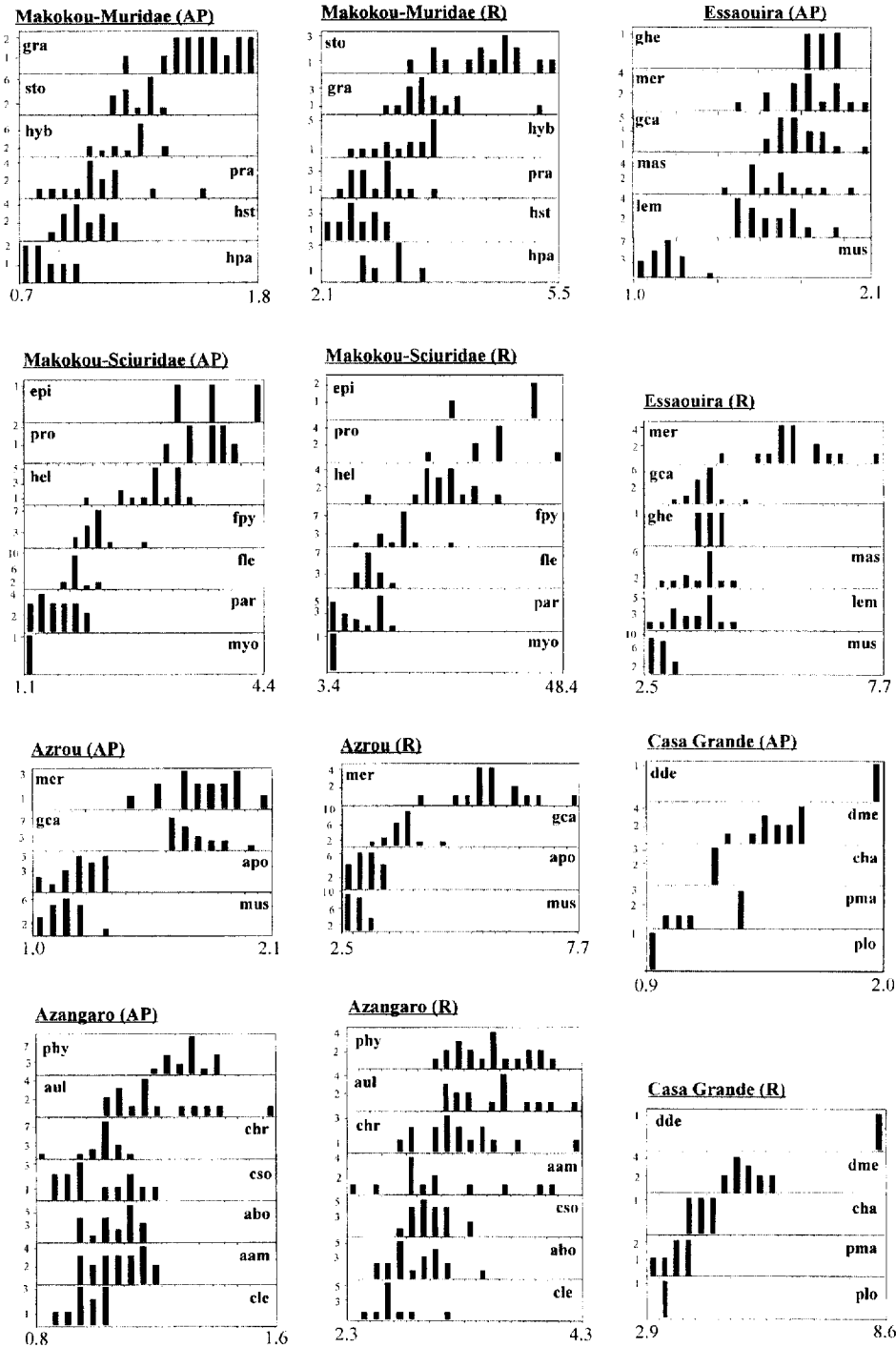
In his study on temporal niche differentiation in carabid beetles, Loreau [22] showed that the fineness of the subdivision of the time scale could have a considerable effect on the results. To test whether there was an effect of the number of classes in the size distributions, we ran simulations for the same data set with several different subdivisions of the size scale (5, 7, 10, 14, 17, 19 and 25 classes). The results for the character AP in the Muridae community from Makokou are provided in *table III*. When the number of classes was too small (5 and 7), the power of the test was low. Increasing the number of classes rapidly led to significant results. Therefore, we chose a number of classes where probability stabilized around 20 for all the following studies.

#### 4.1.2. Effect of smoothing size distributions

Species size distributions should be roughly normally or lognormally distributed. As sampling was not exhaustive, some species presented one or more gaps in their size distribution. One possibility for eliminating gaps was simply to take the outliers out of the

**Table III.** Results of the randomization procedure for the character AP of the Makokou-Muridae community, with unsmoothed and smoothed size frequency distributions and varying number of classes. NC: Number of classes; P: probability of finding a mean overlap that is smaller than or equal to the observed value.

NC	Gaps	Unsmoothed	Smoothed
		P	P
5	no	0.274	–
7	no	0.310	–
10	yes	0.000***	0.000***
14	yes	0.000***	0.003**
17	yes	0.001**	0.004**
19	yes	0.002**	0.001**
25	yes	0.000***	0.000***



**Figure 2.** Species size frequency distributions for the two characters of the upper incisor (AP and R) in the six communities studied. x-axis: Size in mm; y-axis: number of individuals. Abbreviations for species names are the following: hpa, *H. parvus*; hst, *H. stella*; pra, *P. tulbergi*; hyb, *H. univittatus*; gra, *G. rutilans*; sto, *S. longicaudatus*; myo, *M. pumilio*; par, *P. poensis*; fle, *F. lemniscatus*; fpy, *F. pyrrhopus*; pro, *P. stangeri*; hel, *H. rufobranchium*; epi, *E. ebiti*; mus, *M. spretus*; lem, *L. barbarus*; mas, *M. peregrinus*; gca, *G. campestris*; mer, *M. shawi*; apo, *A. sylvaticus*; cso, *C. sorellus*; cle, *C. lepidus*; aam, *A. amoenus*; abo, *A. boliviensis*; chr, *C. jelskii*; aul, *A. pictus*; phy, *P. osilae*; dme, *D. merriami*; dde, *D. deserti*; cha, *C. penicillatus*; plo, *P. longimembris*; pma, *P. maniculatus*.

**Table IV.** Results of the Barton and David's test [4] for the six communities studied.  $G_{1,n}$ : Ratio of the smallest to the largest size ratio;  $G_{1,n-1}$ : ratio of the smallest to the second largest size ratio;  $G_{2,n}$ : ratio of the second smallest to the largest size ratio. These ratios give the three probabilities  $P_1$ ,  $P_2$  and  $P_3$ , respectively. Statistical significance at the 0.05 and 0.01 levels are indicated by \* and \*\*, respectively.

Community	$G_{1,n}$	$P_1$	$G_{1,n-1}$	$P_2$	$G_{2,n}$	$P_3$
Makokou-Muridae (complete community)						
AP	0.11	0.32	0.13	0.49	0.32	0.24
R	0.32	0.05*	0.53	0.04*	0.43	0.11
Makokou-Muridae (without <i>H. parvus</i> )						
AP	0.14	0.25	0.23	0.28	0.33	0.23
R	0.55	0.004**	0.73	0.005**	0.60	0.031*
Makokou-Sciuridae						
AP	0.29	0.03*	0.30	0.09	0.35	0.11
R	0.31	0.02*	0.37	0.05*	0.54	0.01**
Essaouira (complete community)						
AP	0.07	0.49	0.43	0.08	0.08	0.81
R	0.06	0.52	0.12	0.52	0.07	0.87
Essaouira (without <i>M. peregrinus</i> and <i>G. hesperinus</i> )						
AP	0.08	0.54	0.35	0.27	0.23	0.58
R	0.13	0.39	0.26	0.39	0.51	0.18
Azrou (complete community)						
AP	0.08	0.70	0.49	0.70	0.16	0.88
R	0.17	0.46	0.37	0.53	0.47	0.54
Azrou (without <i>A. sylvaticus</i> )						
AP	0.06	0.73	–	–	–	–
R	0.64	0.04*	–	–	–	–
Azangaro						
AP	0.10	0.29	0.12	0.40	0.10	0.64
R	0.09	0.32	0.13	0.35	0.16	0.44
Casa Grande						
AP	0.12	0.42	0.13	0.65	0.74	0.04*
R	0.1	0.47	0.21	0.48	0.34	0.41

data set. However, in this case, we would have neglected some information on the size distribution. Therefore, we smoothed the size frequency distribution by interpolation between two points to eliminate gaps. We then ran simulations for both the unsmoothed and smoothed data sets. There was no significant effect of smoothing on the results (*table III*). We thus used unsmoothed data sets for the following study.

#### 4.2. Results of the B&D and randomization tests for the six rodent communities studied

The species size frequency distributions for the six communities studied are depicted in *figure 2*, and results of the B&D test and randomization procedure are given in *tables IV* and *V*, respectively.

Some general remarks can be made on the results of the two tests. More than half of the cases (twelve out

of twenty, *table V*) were found to be significant for the randomization procedure, while only eleven cases out of the fifty computed (*table IV*) gave probabilities that were under the significance level for the B&D test. Additionally, all but one of the probabilities calculated were below 0.3 which indicates that the results of the randomization procedure are highly non-random. On the contrary, for the B&D test, more than half of the probabilities calculated were above 0.3 (28 cases out of 50).

The first community studied was made up of Muridae from Makokou in the equatorial forest of Gabon. The Muridae from this locality were reviewed by Gauthier-Hion et al. [16] and Duplantier [14] who observed the existence of resource partitioning between coexisting species for both space and food. We selected the six terrestrial, nocturnal and granivorous rodents for this study. In the B&D test, the alternative hypothesis of equal size ratios was moderately

**Table V.** Results of the randomization test for the six communities studied. *P*: Probability of finding a mean overlap that is smaller than or equal to the observed value. Statistical significance at the 0.05, 0.01 and 0.001 levels are indicated by \*, \*\* and \*\*\*, respectively. <sup>a</sup>, Test performed on the uncomplete Casa Grande community without *D. deserti*.

Community	<i>P</i>
Makokou-Muridae (complete community)	
AP	0.002**
R	0.004**
Makokou-Muridae (without <i>H. parvus</i> )	
AP	0.002**
R	0.004**
Makokou-Sciuridae	
AP	0.022*
R	0.145
Essaouira (complete community)	
AP	0.000***
R	0.573
Essaouira (without <i>M. peregrinus</i> and <i>G. hesperinus</i> )	
AP	0.000***
R	0.216
Azrou (complete community)	
AP	0.003**
R	0.154
Azrou (without <i>A. sylvaticus</i> )	
AP	0.000***
R	0.072
Azangaro	
AP	0.058
R	0.000***
Casa Grande	
AP	0.252 (0.001 <sup>a</sup> )***
R	0.155 (0.000 <sup>a</sup> )***

supported for R, the probabilities ranging from 0.04 to 0.11 (table IV). For the other character AP, the null hypothesis was clearly accepted, with probabilities ranging from 0.24 to 0.49. The randomization test led to a clear rejection of the null hypothesis for both characters AP and R (table V). One species in this community, *H. parvus*, was quite rare, representing only 2.5 % of the total captures, while another species of the genus *Hylomyscus*, *H. stella*, was dominant, representing 58 % of the captures [14]. We thus computed the tests after removing *H. parvus* from the data set. The results were still not significant for AP but became more highly significant for R (table IV), all the probabilities decreasing after removing *H. parvus* from the data set. On the other hand, the results of the randomization test remained identical with and without *H. parvus* (table V).

The second community comprised seven arboreal squirrels from the Sciuridae family in Makokou, the same locality in Gabon. These species were studied in details by Emmons [15] who described precisely the squirrels species habits, utilization of space and diet.

In the B&D test, the hypothesis of equal size ratios was moderately supported for both AP and R, with probabilities ranging from 0.01 to 0.11 (table IV). The results were similar in the randomization test, with probabilities of 0.02 and 0.14 for AP and R, respectively (table V).

The third community comes from the sandhills of Essaouira, Morocco, on the edge of the Atlantic ocean. The six rodent species were terrestrial, nocturnal and mostly granivorous, and were studied by Aulagnier [3]. For both characters AP and R, the results led to an acceptance of the null hypothesis in the B&D test, with probabilities ranging from 0.08 to 0.87 (table IV). The results of the randomization test led to a clear rejection of the null hypothesis for size character AP and its acceptance for size character R, with probabilities of 0.00 and 0.57, respectively (table V). However, some paleontological data indicate a late Pleistocene immigration of two species in this community, *M. peregrinus* and the endemic species *G. hesperinus* [3]. In order to test the effect of these recent migrations on community structure, we performed the tests without these two species. In both tests, the results were unchanged compared with those obtained for the complete community, although all probabilities decreased for the character R (tables IV, V).

The fourth community was from Azrou in the Middle-Atlas mountains of Morocco. This community comprised only four species of terrestrial, nocturnal and granivorous rodents [3]. In the B&D test, the hypothesis of equal size ratios was clearly not supported for both AP and R, with probabilities ranging from 0.46 to 0.88 (table IV). The randomization test led to the acceptance of the null hypothesis for size character R and to its rejection for size character AP (table V). As in the previous community, the species *A. sylvaticus* is a recent immigrant in the community of Azrou [3]. Without that species, the results of the B&D test were contrasted, with an acceptance of the null hypothesis for AP and its rejection for R (table IV). The randomization test still led to the rejection of the null hypothesis for size character AP and the result was marginally significant for size character R, with a probability of 0.07 (table V). Thus the tendency was towards rejection of the null hypothesis for size character R in both tests, after removing *A. sylvaticus*. For size character AP, the probability was unchanged in the B&D test and decreased in the randomization test.

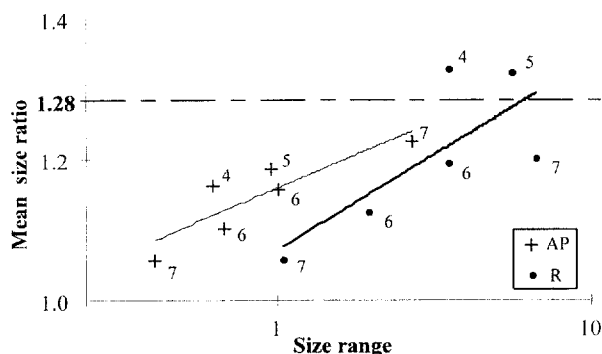
The fifth community studied was from Azangaro, in the Altiplano, Peru. It comprised seven species of

granivorous rodents [24]. For both characters, the hypothesis of equal size ratios was not supported by the results of the B&D test, with probabilities ranging from 0.29 to 0.64 (table IV). On the contrary, the result of the randomization test was very highly significant for R, and marginally significant for AP (table V).

The sixth community came from the Sonoran desert, Arizona, and was studied by Brown [7] and Bowers [5] who evidenced resource partitioning among coexisting desert rodents. It comprised five species of terrestrial and granivorous rodents. Except for one probability ( $P = 0.04$ ), the results of the B&D test led to a clear acceptance of the null hypothesis, with probabilities ranging from 0.41 to 0.65 (table IV). The results of the randomization test led to the acceptance of the null hypothesis for both size characters AP and R, with probabilities of 0.25 and 0.15 respectively (table V). However, the samples for that community were very small, two of the species being represented by only one specimen. There was a great size gap between one of these species, *D. deserti*, and the other species of the community. Without that species, the result of the randomization test became highly significant for both size characters AP and R (table V).

#### 4.3. Variability of size ratios between communities

Figure 3 shows the relationship between the mean size ratio between adjacent species and the overall size range (difference of the mean sizes of the smallest and the largest species) in a community, for the two size characters studied. It appears that there is a strong correlation between the mean size ratio and the logarithm of the size range, with correlation coefficients of 0.87 and 0.75 for AP and R, respectively. This figure also shows that for a given size range, the mean size ratio



**Figure 3.** Relationships between the mean size ratio between species (y-axis) and the total size range in a community (x-axis), for the two size characters studied. Size range is measured in mm on a logarithmic scale. The correlation coefficients are 0.87 and 0.75 for AP and R, respectively. Numbers indicate the number of species in each community.

tends to increase when species diversity decreases. Moreover, most of the ratios in this study are smaller than Hutchinson's [19] theoretical value of 1.28.

## 5. DISCUSSION

### 5.1. Functional meaning of the upper incisor radius

We showed that the results of the B&D test are more often significant when we consider the radius of the upper incisor, R, as compared with its antero-posterior diameter, AP. Since the latter character is well correlated to body size in rodents [25], this supports Dayan and Simberloff's [11] contention that body size is not the best indicator of mammalian community structure.

In addition, the radius of the upper incisor has a great variability in rodents, which is in part independent of body size and can be correlated with their habits. For example, the upper incisor of fossorial rodents have a very low curvature, and this curvature increases from fossorial to terrestrial and arboreal rodents [2]. In the cases studied here, all species are terrestrial (except for the arboreal squirrels from Makokou) and the differences in the incisor radii observed are thus not related to major differences in habits such as those observed between fossorial and arboreal species. However, this does not imply that there are no differences between the terrestrial species studied here. These differences may simply be less pronounced and more gradual from one species to another. The upper incisor radius could consequently be a good indicator of the structure of rodent communities in addition to body size.

In the randomization test, the relationship between values of the probabilities and the size character analyzed seems to be opposite, as the probabilities for size character R were higher than those for size character AP, except for the two communities of Azangaro and Casa Grande. Thus, while the radius of the upper incisor may generate structure in rodent communities, the great variability of this character may prevent it from minimizing size overlaps between species.

### 5.2. Effects of rare species and recent immigrations

We had field capture data only for the Muridae community of Makokou. Removing a rare species from the data set resulted in the B&D test becoming more significant. It seems thus that the presence of a rare species in a community can partly hide its structure. In that sense, McKinney et al. [23] suggested that "rare species participate less in biotic interactions". However, we need more data to test this hypothesis, especially since when few individuals are captured on the field, it does not necessarily mean that the species is effectively rare.

The randomization test was less sensitive to the effect of a rare species in a data set than was the B&D test. If a species is represented by a few individuals in a data set, its niche width will be underestimated. As a consequence, its size overlap with other species and its effect on the results of the randomization procedure will be reduced. On the contrary, the B&D test only takes into account the mean size of each species, irrespective of its relative abundance, thus giving the same weight to all the species in the community.

For the two communities from Morocco, taking into account species that immigrated recently led in most cases to an increase of the probabilities in the two tests, thus increasing the chances of accepting the null hypothesis. Migrations might represent disturbances for community structure, and increase the deviation of a community from its potential equilibrium. More work would be useful to test this hypothesis.

### 5.3. Limiting similarity

In this study, we showed that there was no minimum size ratio between species required for coexistence, contrary to Hutchinson's [19] classical conjecture. Moreover, most of the observed ratios were smaller than Hutchinson's [19] theoretical value of 1.28. Our data show instead that the mean size ratio between species is an increasing function of the total size range and a decreasing function of the number of species in a community. Thus they agree with Abrams' [1] conclusions, who showed that there is no universal limit to the similarity of competing species for their coexistence, and support Simberloff and Boecklen's [26] results who found the Hutchinson's rule to be invalid.

### 5.4. Role of competition

For size character R, in six out of nine cases, the two tests led to the same conclusion of rejection or acceptance of the null hypothesis. For size character AP, only three out of the nine cases led to the same conclusion for the two tests. In the other six cases, the results always led to the rejection of the null hypothesis in the randomization test, whereas the results of the B&D test were not significant. It is important to point out that the null hypotheses are different in the two methods. The B&D tests for equality of size ratios, whereas the randomization procedure tests for minimization of mean size overlap between species. The size structure of a community may be irregular, while at the same time, the mean size overlap between species may be minimum. Reciprocally, the mean size may be spaced regularly without minimizing size overlaps. However, the two patterns share the same common hypothesis, i.e. the impact of interspecific competition on community structure and the two null models represent two methods to test for aspects of

this impact of interspecific competition. In this study, the two tests generally led to similar conclusions for size character R. Thus, when it has a significant impact on community structure, competition appears to both produce a regular size structure and to reduce size overlaps between species for that particular character. For size character AP, the results of the two tests were less consistent, since they were opposite in most cases.

For most of the communities studied, we were unable to consistently reject the null hypothesis that the observed size structure was due to chance. However, in the two communities from Makokou, the tests support both the hypothesis of a regular size structure and the hypothesis of a minimum size overlap between species. These two rodent communities are found in the African equatorial rainforest. Compared with the other communities studied, they experience a more stable environment where changes in temperature and humidity are low. This agrees with the competition theory, which predicts that competitive exclusion or coevolution is more likely in such stable environments, thus generating a structure that is determined by competition.

Lastly, we showed that results of the randomization procedure were highly non-random, all but one of the probabilities calculated being below 0.3. In contrast, more than half of the probabilities calculated for the B&D test were above 0.3. This result suggests that competition may tend to minimize size overlaps between coexisting species, rather than leading to a regular size structure of the community.

## 6. CONCLUSION

Although our results do show some community-wide patterns in agreement with the competition theory, competition does not appear to be always strong enough to both produce a regular size structure and minimize size overlaps between species. Only a few communities, which deserve special attention, led to consistent significant results after performing the two tests. Dayan and Simberloff [11] reached the same conclusion in their study on heteromyid rodent communities. Several factors can affect community structure, some of which have been pointed out in this study, namely, recent immigrations of species in already structured communities and occurrence of rare species. The identification of other potential factors deserves additional research. However, this does not argue against the presence of interspecific competition in rodent communities. Several other authors suggested a regular structure on the basis of body size in rodent communities [6, 7, 9, 18]. Valone and Brown [27] experimentally demonstrated the competitive effect of a dominant species on another one in a desert



rodent community. But communities are open systems, and their organization depends on many internal and external factors. For example, some recent studies on rodent communities showed the importance of predation and habitat use [20]. Community organization should be viewed eventually as the result of many combined effects such as competition, predation, and abiotic factors.

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