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The structure of Congolese shrew ensembles: competition and spatial variation in resource abundance

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Abstract

Interspecific competition, environmental filtering, or spatial variation in productivity can contribute to positive or negative spatial covariance in the abundances of species across ensembles (i.e., groups of interacting species defined by geography, resource use, and taxonomy). In contrast, density compensation should give rise to a negative relationship between ecomorphological similarity and abundance of species within ensembles. We evaluated (1) whether positive or negative covariances characterized the pairwise relationships of 21 species of Congolese shrew, and (2) whether density compensation characterized the structure of each of 36 Congolese shrew ensembles, and did so based on the abundances or biomasses of species. In general, positive covariance is more common than negative covariance based on considerations of abundance or biomass, suggesting dominant roles for environmental filtering and productivity. Nonetheless, negative covariance is more common for ecomorphologically similar species, suggesting a dominant role for competition within functional groups. Effects of abundance or biomass compensation, via pairwise or diffuse competitive interactions, were detected less often than expected by chance, suggesting that interspecific competition is not the dominant mechanism structuring these ensembles. Effects of competition may be balanced by responses to variation in resource abundance among sites in a landscape or among niche spaces within sites. Future studies of compensatory effects should incorporate considerations of heterogeneity in the abundance and distribution of resources in ecological space to better isolate the effects of competition and resource abundance, which can have opposing effects on community structure.

Key words: biomass compensation, Congo Basin, Crocidurinae, density compensation, interspecific competition, lowland rainforest, positive spatial covariance, resource abundance.

Two schools of thought exist concerning the structure of communities and the mechanisms that give rise to it. One focuses on interspecific interactions, especially competition (e.g., Hutchinson 1959; MacArthur and Levins 1967; Chase 2011) or neutral processes within the context of a zero-sum community dynamics (Hubbell 2001), and posits that compensatory processes should lead to negative covariance in population abundances of functionally similar species. The other focuses on species responses to variation in the environment, particularly productivity, and posits that environmental filtering should lead to positive covariance between populations of functionally similar species (Weiher and Keddy 1999; Hubbell 2005).

Competition: compensatory dynamics and negative covariance.

Competitive interactions maintain regularities in community structure by preventing the establishment of species, or

by directing natural selection and favoring phenotypic attributes that reduce niche overlap among species that are associated with limiting resources (Hutchinson 1959; MacArthur and Levins 1967; Chase 2011). Functionally similar species are likely to consume similar resources in analogous ways and in similar habitats (Pfennig and Pfennig 2010). If these species occur in syntopy, this will result in strong interspecific competition if resources are limiting. Given enough time and sufficient intensity, competitive interactions should drive species in a community to either diverge morphologically (character displacement) until interspecific competition is greatly reduced or to be eliminated by competitive exclusion (i.e., local extinction) unless behavioral diversification without morphological correlates arises (Brown and Wilson 1956; Moulton and Pimm 1986; Dayan and Simberloff 2005; Grant and Grant 2006; Pfennig and Pfennig 2010). Interspecific competition may not be sufficiently strong to drive species to extirpation, but may instead result in a reduction in the population sizes of competitors, a process

called density compensation (MacArthur et al. 1972; Stevens and Willig 2000b).

Density compensation is traditionally viewed as evidence that interspecific competition constrains the population density of species that rely on a common limiting resource (MacArthur et al. 1972; Longino and Colwell 2011). Nonetheless, compensatory effects can manifest in different ways. Originally, the density of a single species or the summed density of all species was compared between communities that differed in species richness. For example, if the summed population density (not abundance) of all species on a species-poor island equaled the summed population density of a species-rich mainland site, this would be considered evidence of density compensation as species densities changed to compensate for differences in the richness of sites (MacArthur et al. 1972; Wright 1980). This hypothesis assumes that all species in a community engage in interspecific competition. Furthermore, as variation in density can be influenced by environmental differences between communities beyond species richness, such as the abundance and diversity of resources for which species may compete, compensatory effects can be difficult to identify (Peres and Dolman 2000). Because species that are close in ecomorphological space tend to compete more intensely than do species that are more distant from each other in ecomorphological space, density compensation may be expected within a group of co-occurring species when resources are limiting (e.g., Bowers and Brown 1982; Brown and Bowers 1985). Within this context, the abundances of species should be negatively correlated with ecomorphological similarity to other species (Stevens and Willig 2000a, 2000b). Nonetheless, empirical research on birds (MacArthur et al. 1972; Wright 1980; Lara et al. 2020), bats (Stevens and Willig 2000b; Stevens and Amarilla-Stevens 2012), rodents (Stevens and Willig 2000a), primates (Peres and Dolman 2000), herpetofauna (Rodda and Dean-Bradley 2002; Mesquita et al. 2007), and invertebrates (Bloch and Willig 2010; Longino and Colwell 2011) has provided variable levels of support for the importance of density compensation in structuring animal communities.

Importantly, density compensation is a negative relationship between abundance and functional similarity that manifests within communities (i.e., functionally similar species will have lower abundances than will functionally distinct species in a community). In contrast, negative covariance is a negative relationship between species abundances among communities (i.e., as the abundance of 1 species increases from community to community, the abundance of another species decreases). Nonetheless, both of these phenomena are associated with competition: density compensation represents competition between functionally similar species, whereas negative covariances represent changes in competitive dominance of species.

Resource tracking: positive covariance.

Environmental filtering leads to species with similar niche requirements occurring together in similar habitats (Weiher and Keddy 1999). Moreover, species should be selected for growth and survival in the most common environmental conditions regardless of how many other species are also adapted to those conditions (Hubbell 2005). This results in more species and more abundant species being adapted to common environmental conditions or to highly productive niche spaces compared to less common environmental conditions or less productive niche spaces (Hubbell 2005). Consequently, environmental filtering should result in

functionally similar species evincing similar responses to environmental variation, leading to positive covariance in species abundances in time or space. Such shared responses to variation in resource availability indicate that competition is not the dominant structuring mechanism, resulting in random associations between functional similarity and species abundance.

Abundance versus biomass.

An implicit assumption underlying studies of density compensation is that compensatory mechanisms associated with interspecific competition are demographic in nature, such that abundance is a useful metric for assessing the strength of interspecific competition as a structuring mechanism. However, transforming the number of individuals into species-level biomass may create a more sensitive metric for assessing compensatory effects (i.e., biomass compensation) associated with interspecific competition for 2 reasons (Arakaki and Tokeshi 2019). First, variation in productivity more commonly influences structure compared to interspecific competitive interactions, making compensatory effects based strictly on abundance potentially rare (Houlahan et al. 2007). Second, species abundance and body size are negatively correlated (Ulrich 2008); therefore, all other things being equal, smaller species attain greater population densities than do larger species that use a common limiting resource. Critically, individuals of different species are not equivalent in terms of their impact on resources or of their responses to changes in resource abundance. Indeed, much of competition theory formalizes the differential competitive effects of different species via incorporation of "competition coefficients" (MacArthur 1968; Lawlor 1980). Ideally, competition coefficients are based on species-specific metabolic rates. However, these rates, whether determined in laboratory conditions or in the field, are unavailable for most species (Gliwicz and Taylor 2002). In contrast, body mass is a standard morphological measurement taken for vertebrate specimens during field research and mean body mass estimates are typically available for most species. Although metabolic differences exist among species and among individuals of different sizes of the same species, relative biomass should better estimate interspecific competitive effects compared to relative abundance.

Interacting species.

We follow the scheme of Fauth et al. (1996) in referring to geographically defined groups of interacting species as communities (e.g., all species on an island), and groups of interacting species defined by geography, resource use, and taxonomy as ensembles (e.g., all frugivorous bats on an island). We assess density or biomass compensation at the level of ensembles, as this is the focal group within which competitive effects should be most intense and mediated by a suite of homologous morphological characteristics.

Focal taxon.

Shrews (Soricidae) represent a useful model for evaluating the roles of competition and productivity in structuring ensembles via positive or negative covariation in abundance or biomass, or via density compensation. Although interspecific competition may be intense among syntopic soricids (i.e., all are primarily terrestrial insectivores), shrews exhibit few of the characteristics that facilitate resource partitioning that are apparent in other groups of small mammals. For example, shrews exhibit relatively
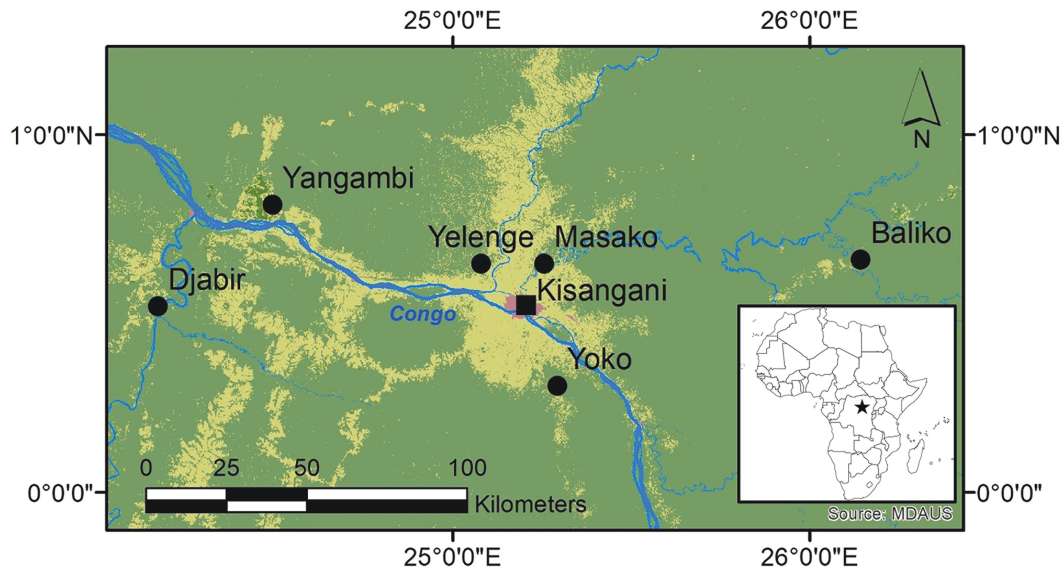
Fig. 1. Sampling localities (dots) in the environs of Kisangani (Table 2). The city of Kisangani (square) is surrounded by a mosaic of agricultural land and regrowth forest (light green), whereas old-growth forests (dark green) occur throughout the area. The Congo River and its tributaries appear in blue. Inset shows the location of the study area in Africa.

little differentiation in adaptive physiology, habitat preferences, or temporal activity (Kirkland 1991). Consequently, syntopic shrew populations that share resource bases could potentially exhibit compensatory effects rather than strong competitive forces leading to exclusion. Density compensation was not observed in populations of *Sorex minutus* in Ireland (species richness is 1) compared to populations in the Netherlands (species richness is 2), where *S. minutus* is sympatric with *S. araneus* (Ellenbroek 1980). Nonetheless, in a study of density compensation in *S. araneus* and *S. minutus*, Malmquist (1986) reported a higher population density of *S. minutus* in allopatry than in sympatry. Shrews are opportunists in terms of the number of consumed prey species, but generally specialize via quantitative (i.e., how much they consume of each prey type) rather than qualitative (the identity of prey types that they consume) differences in diet (Churchfield 1991, 1994; Ivanter et al. 2015).

We use data from 21 species of shrew from 36 sites in the Congo Basin to evaluate the roles of competition and resource abundance in structuring shrew ensembles, and do so based on considerations of abundance and biomass. Shrew ensembles in the Congo Basin exhibit niche expansion rather than species packing, suggesting that the functional volumes of shrew ensembles may be affected more by environmental filtering than by competition (Van de Perre et al. 2020). We evaluate 2 hypotheses. First, shrew populations should exhibit positive rather than negative covariance in abundance or in biomass. This prediction is based on the expectation that changes in productivity will have similar effects on shrew species (i.e., greater productivity will result in greater abundance of all or most shrew species) rather than differences in habitat quality positively affecting some shrew species while negatively affecting other shrew species, leading to habitat specialization. Second, because shrews are generalist insectivores that facilitate coexistence by consuming different proportions of shared prey types rather than different prey, density compensation should be rare. This is based on the expectation that variation in resource availability for particular niche spaces will obfuscate effects of competition (i.e., that competition is not the dominant structuring mechanism for these ensembles).

Materials and methods
Shrew ensembles.

We compiled data for shrews from 3 studies in the area around Kisangani in the Democratic Republic of the Congo (Gambalemoke et al. 2008; Mukinzi 2014; Van de Perre et al. 2018). Importantly, all previous studies of density compensation have been conducted on soricine shrews, whereas Congolese shrews are members of the Crocidurinae. This subfamily of shrews is largely tropical and generally has more species-rich and functionally diverse ensembles compared to soricine counterparts. Indeed, the dramatic diversification of crocidurines should make them more susceptible to compensatory effects (Churchfield et al. 2004). The combined data represent 36 ensembles (i.e., sites) distributed within 6 general areas in Tshopo Province (Fig. 1). Sampling localities are separated by the Congo River and its major tributaries (Tshopo, Lindi, and Lomami rivers). Because the data set of Yoko contained multiple trapping sessions for each site, we used only a single session per site and selected sessions that were executed during 1 season and avoided transition periods between seasons. When multiple seasons remained for a particular site, we chose the trapping session with the highest total abundance of shrews to ensure the best possible estimate of ensemble composition. The final data set comprises 1,289 individuals representing 21 species. Mean body mass ranged from 2.05 g (*Suncus* cf. *remyi*, $n = 30$) to 45.5 g (*Crocidura goliath*, $n = 10$).

At all sites, shrews were sampled using the paceline method (Martin et al. 2001), which involved placing 20 pitfall traps at 5-m intervals along transects (Nicolas et al. 2003). Pitfall traps consisted of nonbaited buckets (30-cm deep) buried so that the rims were even with ground surface. A plastic drift fence (100 m) was used to increase capture effectiveness by guiding shrews toward traps. Pitfall traps were maintained for 21 days, with animals removed daily. Shrews were euthanized and standard measures of external morphology were taken. Species were identified based on external morphology and craniodental characteristics (Van de Perre et al. 2019). Pitfall trapping is the most effective protocol for shrew sampling, and captures more individuals and species of shrew than any other trapping method (Nicolas

et al. 2003; Gambalemoke et al. 2008). By comparing the results of 2 trapping sessions conducted in 2 consecutive years, Nicolas et al. (2003) concluded that removal trapping did not adversely affect local population numbers or species richness of shrews. Moreover, because trapping sessions were short in duration, the data would not be influenced by demographic responses to the removal of individuals during a trapping session. When necessary, species assignments were verified through comparison of 16S rRNA sequences with a reference DNA barcode library. Specimens belonging to species complexes in need of revision were provisionally given cheironyms, pending formal description. Specimens are stored at the Laboratory of Ecology and Animal Resource Management, University of Kisangani. Tissue samples are stored at the University of Antwerp and at the Royal Belgian Institute of Natural Sciences.

Ecomorphological structure.

To estimate the strength of interspecific competition, we selected a set of morphological characteristics that reflect ecological functioning of shrews (Supplementary Data SD1). These "ecomorphological" traits comprised external and cranial characteristics. External characteristics included mass (M) and length of head and body (HB), tail (T), hind foot (HF), and ear (E). Cranial characteristics included condyloincisive length (CI), greatest width of skull (GW), interorbital width (IW), length of upper tooth row (UTR), and length of lower tooth row (LTR). Because most morphometric data are correlated strongly with body size, we used relative measures to characterize function—T, HF, and E were each divided by HB, whereas GW, IW, UTR, and LTR were each divided by CI.

Averages were determined for each species using our data for external measures and data from the literature for cranial measures (Supplementary Data SD2). Because the removal of outliers generally increases accuracy and reduces errors of inference (Osborne and Overbay 2004), outliers (i.e., observations that are outside the 1.5 |*| the interquartile range, the difference between 75th and 25th quartiles) were removed from analyses. In general, these outliers likely resulted from measurement or transcription errors, or from pregnancies in the case of body mass. Outliers represented <3% of all measurements, and effects of outlier removal were generally small (means for 90% of measurements changed <2% compared to means that included outliers). These adjusted trait values were used to calculate pairwise, multidimensional, functional distances between species using the Gower metric from the "vegan" package in R (Oksanen et al. 2022).

Competitive scenarios.

Ecological structure can be produced via a spectrum of interspecific competitive interactions, ranging from pairwise interactions between the most similar species, to those based on diffuse interactions among all species in a community or ensemble (Stevens and Willig 2000a). Indeed, ensembles may be the ecological grouping for which effects of competition or resource tracking are most easily detected because species are syntopic (i.e., interact locally), share common resources (i.e., species are in the same guild), and possess morphological characteristics that have similar functional consequences because of shared evolutionary history of the focal taxon. If diffuse competition is the pervasive mechanism that structures an ensemble, then the abundance or biomass of a species should be influenced by its ecomorphological proximity to all other species. Diffuse competition presumably occurs when all species have relatively general resource requirements and

when their resource bases are shared with species that occupy similar ecomorphological space. This scenario was represented as the sum of Euclidean distances between a focal species and each of the other species in the ensemble in ecomorphological space (total neighbor distance, TND). In contrast, interactions between a species and its most ecomorphologically similar neighbor (hereafter pairwise competition)—presumably the species for which competitive interactions are strongest—may be the primary factor determining structure, and the ecomorphological distance between a species and its nearest neighbor should most affect abundances or biomasses of species. This scenario should occur more often when species possess narrow resource requirements and resource overlap involves few species. This scenario was represented as the Euclidean distance between each species and its nearest ecomorphological neighbor in the ensemble (nearest neighbor distance, NND).

Statistical analyses.

To visualize ecomorphological relationships among species in 2-dimensional space, we executed nonmetric multidimensional scaling (NMDS) based on Gower distances using the "vegan" package in R (Oksanen et al. 2022). In addition, hierarchical clustering analysis based on Ward's method and Gower distances identified ecologically relevant species groups.

We evaluate the prevalence of positive or negative covariance between each possible pair of shrew species for the 36 study sites separately based on each of 4 characteristics: relative abundance; relative biomass; absolute abundance; and absolute biomass. For each characteristic, assessment of covariance between species involved a 3-step process of multivariate and univariate analyses. First, we evaluated multivariable evidence for nonrandom associations by comparing an empirical correlation matrix to an identity matrix of the same rank—1s along diagonals and zeros otherwise (covariances) via Bartlett's Test of Sphericity (1951). Significance in this context means that the overall correlation matrix represents more significant associations than expected by chance. Second, if Bartlett's Test was significant, we tested whether the distribution of positive associations and negative associations was different from chance expectations by using a Binomial Test (Sokal and Rohlf 2012), with the likelihood of a positive correlation equal to the likelihood of a negative correlation (0.5), and the number of possible interspecific correlations equaling 210 ($K * [K - 1]/2 = 21 * 20/2$, where K is the number of species). This allows us to evaluate if the preponderance of correlations were directional, either positive or negative, regardless of their individual levels of significance. Finally, to identify particular interspecific correlations that likely contributed to multivariate significance, we executed Pearson product-moment correlation analysis (Sokal and Rohlf 2012) for each possible pair of species.

Separately for each of 36 shrew ensembles, we evaluated compensatory effects associated with interspecific competition following Stevens and Willig (2000b). Compensatory effects were expressed in terms of relative abundance (Supplementary Data SD3) or relative biomass (Supplementary Data SD4). Relative abundances were calculated for each ensemble by dividing the number of individuals of each species in an ensemble by the total number of individuals in that ensemble. Relative biomass of a particular species in an ensemble equals the product of its relative abundance in that ensemble and its average body mass, divided by the sum of the products of such terms for all species in that ensemble. For each ensemble, we quantified the Pearson product-moment correlation coefficient for compensatory effects

(based on either relative abundance or relative biomass) for each of 2 competitive scenarios (i.e., pairwise [NND] or diffuse [TND] competition).

To determine if compensation characterized an ensemble (i.e., whether empirical correlations were greater than expected by chance), we compared the correlation coefficient from each empirical ensemble to a distribution of correlations produced by a stochastic process. While preserving the integrity of the ecomorphological relationships among species within an ensemble, abundances or biomasses were assigned at random to species. A correlation coefficient was then calculated between randomized values and empirical ecomorphological distances within the simulated ensemble. One thousand iterations of this process yielded a probability density function for subsequent hypothesis tests. The correlation coefficient from the empirical ensemble was compared to the probability density function of simulated correlation coefficients ($\alpha = 0.05$). If the empirical coefficient occurred within the upper 5% of the distribution of simulated coefficients, a nonrandom positive association characterized the relationship between ecomorphological distance and abundance or biomass, consistent with compensation.

To evaluate the overall evidence of compensatory effects based on all 36 ensembles, we used 2 approaches to conduct meta-analyses. First, we conducted meta-analyses for each combination of competitive scenario (diffuse competitions or pairwise competition) and metric (relative biomass or relative abundance) via Stouffer's method. Stouffer's method was executed using the sumz function from the "metap" package in R (Dewey 2022). Second, we used paired *t*-tests to evaluate whether correlation coefficients differed significantly between density metrics

(relative abundance vs. relative biomass) or between competitive scenarios (diffuse vs. pairwise competition) for the suite of ensembles.

Results

The relative position of species in 2-dimensional ecomorphological trait space was visualized using NMDS (Fig. 2a; stress = 0.11). Hierarchical clustering based on ecomorphological data resulted in 4 distinct functional groups (Fig. 2b) associated with variation in foraging habits and habitat preferences of species. Large shrew species with small ears (Kingdon 2013) that forage in leaf litter and under logs comprised the first functional group (blue in Fig. 2); tiny species with relatively broad skulls formed a second group (green in Fig. 2); species with relatively large feet, tails, and ears, suggesting an arboreal lifestyle (Kingdon 2013), formed a third group (purple in Fig. 2), and finally, generalist species with traits of intermediate magnitude formed a fourth group (red in Fig. 2).

Correlation matrices evaluating covariance between species of shrews based on relative abundance, relative biomass, absolute abundance, or absolute biomass each exhibited significant nonrandom associations (all *P*-values < 0.001). In addition, the distribution of positive and negative correlation coefficients differed significantly from chance (i.e., a 1:1 ratio) for each of the 4 characteristics ($P = 0.013$ for relative biomass and $P < 0.001$ for relative abundance, absolute abundance, and absolute biomass). In each case, significantly more negative correlations occurred than positive correlations. In contrast to the preponderance of negative correlation values, significant associations were predominantly for positive correlations, with significant
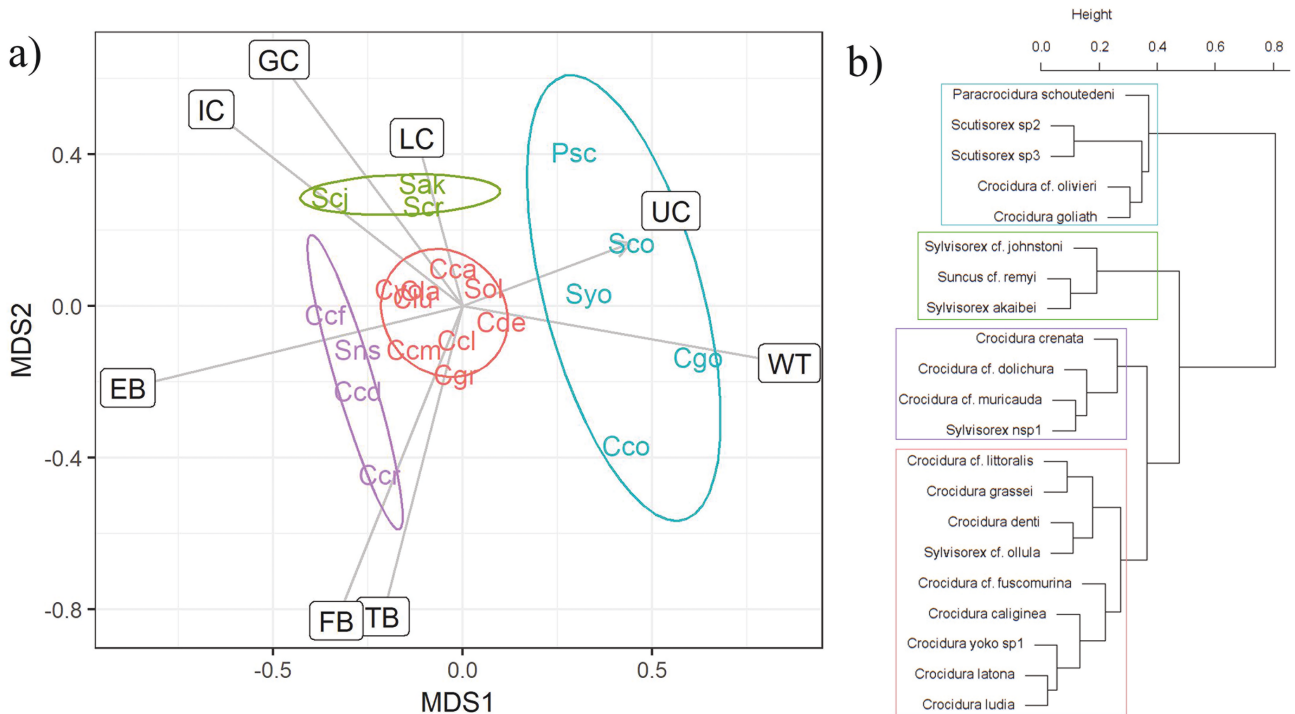
Fig. 2. Ecomorphological position of shrew species in functional trait space defined by NMDS (panel a) and hierarchical clustering of shrew species based on those same ecomorphological traits (panel b). Colors refer to functional groups derived from hierarchical clustering. Vectors represent the correlation of each trait with species values. Species codes: Cca, *Crocidura caliginea*; Ccd, *Crocidura* cf. *dolichura*; Ccf, *Crocidura* cf. *fuscomurina*; Ccl, *Crocidura* cf. *littoralis*; Ccm, *Crocidura* cf. *muricauda*; Cco, *Crocidura* cf. *olivieri*; Ccr, *Crocidura crenata*; Cde, *Crocidura denti*; Cgo, *Crocidura goliath*; Cgr, *Crocidura grassei*; Cla, *Crocidura latona*; Clu, *Crocidura ludia*; Cyo, *Crocidura yoko* sp1; Psc, *Paracrocidura schoutedeni*; Syo, *Scutisorex yokoensis*; Sco, *Scutisorex congicus*; Scr, *Suncus* cf. *remyi*; Sak, *Sylvisorex akaibei*; Scj, *Sylvisorex* cf. *johnstoni*; Sol, *Sylvisorex* cf. *ollula*; Sns, *Sylvisorex* nsp1. For trait codes, see Materials and methods.

positive covariances occurring twice as often as significant negative covariances for relative measures (i.e., abundance or biomass), and 10 times as often as significant negative covariances for absolute measures (Table 1). Significant positive covariance occurred about twice as often as expected by chance at α of 0.05 regardless of whether comparisons were made between species belonging to the same functional group or between species belonging to different functional groups (Table 1). In contrast, significant negative covariance only occurred more often than expected by chance for comparisons within functional groups based on relative measures.

We detected compensatory effects that are indicative of strong competition (experiment-wise error rate: α = 0.05) in only 4 analyses involving 3 of 36 ensembles: 1 based on relative abundance and 3 based on relative biomass, including 1 case in which compensatory effects were indicated based on NND and TND (Table 2). This number of compensatory effects (4) is less than that expected by chance (i.e., 0.05 * 144 analyses = 7.2).

Correlation coefficients based on relative biomass were larger than those based on relative abundance in corresponding ensembles, regardless of competitive scenario (NND, t = −8.35, $P < 0.001$; TND, t = −9.15, $P < 0.001$), with higher correlation coefficients associated with relative biomass in 92% of ensembles in pairwise competition (i.e., NND) scenarios and in 94% of ensembles in diffuse competition (TND) scenarios. This suggests that biomass may be more effective than abundance in detecting competitive effects, even when such effects are weak. Meta-analysis via Stouffer's method found no evidence of density compensation when considering all 36 ensembles as a group (Table 2). Correlation coefficients were generally greater for pairwise (NND) compared to diffuse (TND) competitive scenarios, significantly so based on biomass (t = 2.10, $P = 0.043$) and approaching significance based on abundance (t = 1.73, $P = 0.093$).

Discussion

In general, compensatory mechanisms associated with interspecific competition have been assumed to be demographic in nature, with abundance representing a useful metric for assessing the strength of competition as a structuring mechanism. Density compensation is based on the premise that a particular species will be more abundant if it experiences less interspecific competition (Root 1973; Hawkins and McMahon 1989). However, number of individuals may be a poor measure of the ecological or evolutionary responses of species, as not all species require the same per capita quantity of resources. Although species-specific metabolic rates (e.g., differential resource needs) are often unavailable, biomass is generally known for each species and may represent a suitable measure for assessing compensatory effects. A meta-analysis of our results suggest that biomass is a more sensitive indicator of compensatory effects than is the number of individuals (Table 2); however, this sensitivity does not change the general conclusion that competition is not the dominant structuring mechanism in Congolese shrew ensembles.

Congolese shrew ensembles exhibited more frequent negative covariance between species pairs (evidence of competition) than positive covariance (evidence for resource tracking); however, these associations were rarely significant and suggest weak evidence of competition influencing the abundance or biomass of species. In contrast, significant positive covariance between pairs of species was much more common than was significant negative covariance, suggesting that responses to resource tracking are stronger than are effects of competition for particular pairs of species. In combination, these results are consistent with a meta-analysis that concluded that compensatory effects are rare and often weak in natural communities (Houlahan et al. 2007). The preponderance of weak negative covariances could represent species-specific responses to variation in habitat quality or type. For example, species A may

Table 1. For each of 3 groups (i.e., pairs of species within functional groups, pairs of species that represent different functional groups, or all species regardless of functional group affiliation), the proportion of the total number of pairwise comparisons that exhibited positive covariance, negative covariance, or either response (total) based on relative abundance, relative biomass, absolute abundance, or absolute biomass.

	Within functional group	Between functional groups	All species
Relative abundance			
Positive covariance	10.9%	11.6%	11.4%
Negative covariance	7.3%	5.2%	5.7%
Total	18.2%	16.8%	17.1%
Relative biomass			
Positive covariance	9.1%	10.3%	10.0%
Negative covariance	9.1%	2.6%	4.3%
Total	18.2%	12.9%	14.3%
Absolute abundance			
Positive covariance	10.9%	12.3%	11.9%
Negative covariance	1.8%	0.6%	1.0%
Total	12.7%	12.9%	12.9%
Absolute biomass			
Positive covariance	10.9%	12.3%	11.9%
Negative covariance	5.5%	0.6%	1.9%
Total	16.4%	12.9%	13.8%

Table 2. Empirical Pearson correlation coefficients (*R*) and probabilities that the empirical coefficient is no greater than what would be expected by chance (*P*), as well as meta-analyses (based on sumz statistic, z in table) conducted via Stouffer's method (Dewey 2022). Significant positive correlations (*P* ≤ 0.05) consistent with compensation are bold. NND refers to the nearest neighbor distance scenario, whereas TND refers to the total neighbor distance (see text for details).

Locality	Relative abundance				Relative biomass			
	NND		TND		NND		TND	
	R or z	P	R or z	P	R or z	P	R or z	Pj
Babogombe_FP_L1_S5	−0.503	0.974	−0.359	0.818	−0.360	0.806	−0.258	0.682
Babogombe_FP_L2_S1	−0.458	0.751	−0.207	0.552	−0.019	0.540	0.228	0.282
Babogombe_FP_L3_S5	−0.489	0.937	−0.333	0.904	−0.254	0.727	−0.044	0.475
Babogombe_FPG_L1_S7	−0.195	0.633	−0.184	0.543	0.618	0.116	0.622	0.103
Babogombe_FPG_L2_S5	−0.286	0.762	−0.153	0.545	0.198	0.311	0.323	0.230
Babogombe_FS_L1_S1	−0.381	0.766	−0.382	0.799	−0.096	0.536	−0.199	0.636
Babogombe_FS_L2_S1	−0.067	0.564	0.066	0.437	0.459	0.113	0.459	0.148
Babogombe_JJ_L1_S3	0.201	0.337	−0.027	0.501	0.164	0.361	0.314	0.267
Babogombe_JV_L1_S3	−0.215	0.761	−0.169	0.604	0.585	0.117	0.328	0.300
Babogombe_JV_L2_S1	−0.497	0.918	−0.591	0.924	−0.328	0.708	−0.309	0.737
Baliko_FP	0.143	0.374	0.386	0.173	0.435	0.143	0.604	**0.036**
Baliko_FS	−0.436	0.882	−0.307	0.794	0.449	0.124	0.326	0.233
Baliko_JC	0.244	0.264	0.075	0.433	0.892	**0.014**	0.788	**0.023**
Djabir_FP_L1	0.002	0.498	−0.418	0.872	0.063	0.413	−0.380	0.812
Djabir_FP_L2	−0.349	0.757	−0.534	0.852	0.330	0.281	0.198	0.356
Djabir_FS	−0.500	0.807	−0.613	0.883	0.018	0.480	−0.159	0.640
Kisesa_JJ_S5	−0.373	0.756	−0.341	0.734	0.198	0.344	0.130	0.375
Kisesa_JV_S7	−0.427	0.784	−0.610	0.915	0.255	0.245	0.159	0.305
Masako_FS_L1A	−0.403	0.865	−0.401	0.850	0.337	0.181	0.184	0.316
Masako_FS_L1C	−0.078	0.595	−0.163	0.655	0.169	0.317	0.134	0.355
Masako_Gil_L1A	−0.543	0.951	−0.452	0.922	0.172	0.315	0.210	0.271
Masako_Gil_L1C	−0.639	0.954	−0.451	0.884	0.164	0.452	0.323	0.324
Yangambi_BRA1	0.875	**<0.001**	0.763	0.074	0.633	0.142	0.539	0.287
Yangambi_GIL3	−0.116	0.547	−0.210	0.659	0.444	0.106	0.336	0.155
Yangambi_GIL4	−0.123	0.413	−0.180	0.563	−0.008	0.232	−0.074	0.425
Yangambi_JEU1	−0.303	0.797	−0.493	0.946	0.264	0.206	0.147	0.304
Yangambi_JEU2	−0.340	0.857	−0.376	0.886	−0.084	0.528	−0.139	0.641
Yangambi_JEU3	−0.040	0.371	−0.304	0.747	0.416	0.163	0.145	0.291
Yangambi_JEU4	−0.324	0.823	−0.383	0.902	−0.026	0.371	−0.095	0.474
Yangambi_JEU5	−0.041	0.294	−0.296	0.774	0.278	0.145	−0.035	0.438
Yangambi_MIX2	−0.776	0.888	−0.666	0.888	0.096	0.411	0.243	0.370
Yangambi_MIX3	−0.618	0.939	−0.850	1.000	−0.199	0.695	−0.421	0.843
Yangambi_MIX5	0.409	0.184	0.275	0.250	0.870	0.058	0.820	0.100
Yangambi_MIX6	0.036	0.321	−0.038	0.400	0.624	0.074	0.583	0.092
Yelenge_FP	0.052	0.433	−0.110	0.607	−0.266	0.684	−0.280	0.718
Yelenge_FS	−0.283	0.720	−0.455	0.899	−0.212	0.640	−0.397	0.829
Meta-analysis	0.621	0.267	0.636	0.262	−0.469	0.680	−0.728	0.767

do better in habitat A, whereas species B does better in habitat B, resulting in negative covariances in the abundances or biomasses of these species. However, the paucity of site-specific details on relevant habitat characteristics or resource abundances makes drawing conclusions about the biological bases of these patterns controvertible. Within the context of relative abundance or biomass, significant positive covariance (i.e., mutual increases in abundances or biomass of ecomorphologically similar species) suggests that common responses to variation in resource availability often counteract effects of competition. Nonetheless, little evidence suggests that resource abundance differentially affects particular species based on

their positions in ecomorphological (functional) space (Table 1). Rather, greater resource abundance has a similarly positive effect on shrew species regardless of their functional niche, likely obscuring effects of competition.

In the case of Congolese shrews, higher correlation coefficients for relative biomass than for relative abundance may arise because of the positive correlation between mass and average NND: larger species are farther from their closest ecomorphological neighbors in these ensembles compared to the situation for smaller species (Fig. 3). In terms of biomass, species with close ecomorphological neighbors (i.e., low NND) contribute less biomass to the ensemble compared to their contributions to abundance, whereas species with distant nearest ecomorphological neighbors (i.e., high NND) contribute more biomass to the ensemble compared to their abundance contributions. Consequently, the slope of the relationship is more positive based on biomass than it is based on abundance. In those ensembles in which compensation occurs, *C.* cf. *olivieri* is the most dominant species, either in terms of relative abundance (Supplementary Data SD3) or relative biomass (Supplementary Data SD4). Because this species has the second highest mean NND within the species pool, its dominance in an ensemble increases the probability of finding a positive correlation between relative abundance or biomass and ecomorphological distance.

Although shrews are known to be wide-spectrum feeders (i.e., euryphagous insectivores), the diet of each species is dominated by a few major prey taxa that are common and abundant (Churchfield 1991, 1994; Dudu et al. 2005). The daily energy requirements of shrews dictate that individuals must forage effectively and frequently to survive (Churchfield 1994). Given such elevated energy constraints, shrews cannot afford to be highly selective foragers, with encounter rates being a key factor in prey consumption. As a result, tropical shrews mainly feed on ubiquitously abundant ants and termites, even though these taxa have low energy content compared to other insects (Churchfield 1994; Dudu et al. 2005). In tropical forests, arthropod abundance decreases with increasing body size (Stork and Blackburn 1993). Therefore, tropical shrew species with intermediate morphological traits (i.e., the generalist functional group), which are located near the center of ecomorphological space

(Fig. 2), may have a fitness advantage compared to peripheral species in the sense that their intermediate traits enable them to efficiently feed on a wider range of prey sizes compared to species with more extreme trait values (i.e., small or large shrew species). Many shrew ensembles are dominated by multiple generalist species, which contrasts with the predictions of competition theory and the expectation of density compensation. In contrast, large species are more likely to forage for larger, less abundant invertebrates, as well as small vertebrates (including shrews), making large shrews more vulnerable to changes in habitat quality or food availability. This may explain why the largest shrew species (*C. goliath* and *Scutisorex* spp.) only occur in high-productivity environments such as tropical rainforests (Kingdon 2013).

Because shrews have a high metabolic rate as well as limited capacities to store energy (McNab 1991), it is logical that competition for resources will be reflected in the total biomass of a population. Nonetheless, pairwise (i.e., NND) competitive scenarios consistently rendered higher correlation coefficients than did diffuse (i.e., TND) competitive scenarios (Table 2). Despite a lack of resource partitioning in the types of consumed prey, the preferred prey type depends on shrew body size (Churchfield 1994; Dudu et al. 2005). This relationship between preferred prey size and body size in shrews may explain: (1) why negative covariance occurs more often than expected by chance within functional groups, but not between species from different functional groups; and (2) why compensatory effects manifest more strongly for pairwise than for diffuse competition scenarios.

Our results highlight the importance of knowledge about resource use and resource availability. Resources in a local area are not distributed evenly with respect to the ecomorphological space occupied by members of a community or ensemble. The rarity of significant correlations between ecomorphological distances and the abundances (or biomasses) of species (i.e., compensatory effects) could arise because different quantities of resources are associated with different regions of ecomorphological space (i.e., heterogeneity in resource availability), with abundances (or biomasses) of consumers reflecting variation in resource quantity rather than proximity to other species. As such,
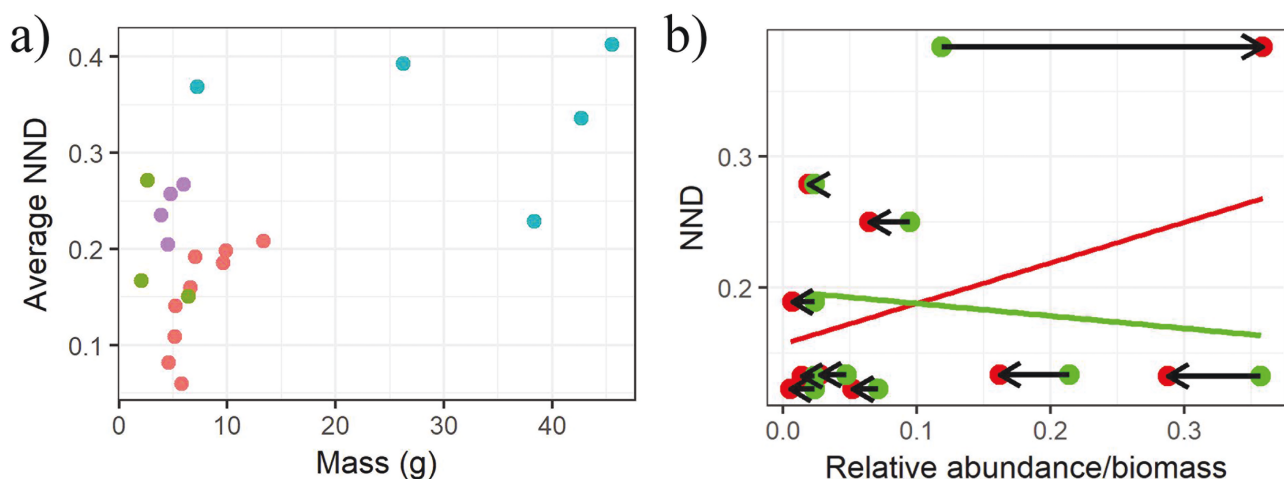
Fig. 3. Average nearest neighbor distance (NND) of species within ensembles increases ($R = 0.60$; P-value $= 0.004$) with average ensemble mass (panel a). Colors indicate functional groups (Fig. 2b). The importance of particular species in affecting NND (panel b) is illustrated for 1 site (Yangambi_GIL3) based on the metric reflecting relative abundance (dots at beginnings of arrows) versus relative biomass (dots at ends of arrows). Arrows indicate the change in relative importance of each species if weighted by abundance versus weighted by biomass. Least-squares lines from regression analysis show the relationship between NND and relative abundance (decreasing) or relative biomass (increasing).

species could be excluding each other from areas of ecomorphological space, but their abundances are determined primarily by resource abundance associated with the space that they occupy rather than with ecomorphological proximity to other species. Moreover, apparently random patterns may represent a balance between these opposing mechanisms. More specifically, if responses to productivity lead to negative associations between ecomorphological distance and abundance or biomass, and compensation has the opposite effect, a balance of these 2 mechanisms would produce a pattern that is indistinguishable from random associations (Table 2).

Future studies of compensatory effects would benefit from incorporation of information on the distribution of resources used by members of a community or ensemble, and when possible, should consider the entire group of species known to use a particular resource base (i.e., a local guild). However, this too has challenges, as analogous morphological traits likely do not characterize different taxonomic subsets of local guilds (i.e., ensembles) or may not reflect the same functions (e.g., traits that measure a particular function are different for granivorous birds, rodents, and ants).

Comparisons between studies on density compensation are complicated by autecological differences among focal taxa, environmental differences among study areas, and interactions between these 2 sources of variation. Nonetheless, 1 generality that arises from studies that used similar approaches to evaluate density compensation (Stevens and Willig 2000a, 2000b; Stevens and Amarilla-Stevens 2012; this study) is that ensembles in low-productivity environments (Stevens and Willig 2000a) likely experience more intense competition due to low resource availability leading to compensatory effects. In contrast, highly productive environments may have fewer limiting resources for which species compete, reducing the effects of interspecific competition on the structure of communities or ensembles over ecologically relevant temporal scales (e.g., Stevens and Willig 2000b; Stevens and Amarilla-Stevens 2012; this study). Importantly, all of these studies reflect ensemble-level analyses, with fewer ensembles likely composing local guilds in low-productivity environments compared to high-productivity environments (i.e., fewer groups feed on seeds in deserts than on insects or fruit in tropical rainforests). Consequently, ensemble-level analyses encompass a larger portion of the local guild that competes for limiting resources in low-productivity environs.

Given the diversity of prey species used by insectivores, the diversity of insectivorous species, and the inherent ecological differences in these groups of prey and predators, studies of compensation in insectivores will generally be confounded with heterogeneity in the distribution of resources (especially in highly diverse environments such as tropical rainforests), making patterns of compensation difficult to detect or interpret. These dynamics likely are responsible for the paradoxical patterns observed for Congolese shrew ensembles, with negative covariances occurring significantly more often than positive covariances, but with positive covariances being significant much more often than are negative covariances. The greater the heterogeneity in resources (a factor that contributes to the diversity of prey species), the more difficult it becomes to discern patterns associated with compensation from those associated with variation in the availability of different types of resources. Furthermore, in analyses focusing on a particular taxon (an ensemble rather than a local guild), interactions with species outside of the focal taxon may mold ecomorphological patterns as much as do interactions within the focal taxon (e.g., rodents

may also compete with ants and birds for seeds). To effectively evaluate compensatory effects, future research should focus on well-known or well-defined resource bases, conditions that are more easily found in low-production environments (Stevens and Willig 2000a) or laboratory conditions (Mcgrady-Steed and Morin 2000; Jiang 2007).

In conclusion, neither competition nor resource abundance represent a dominant mechanism that structures Congolese shrew ensembles, with opposing effects leading to nuanced and paradoxical patterns both within and among ensembles. Nonetheless, incorporation of biomass into metrics used to evaluate compensatory effects holds considerable promise for quantification of the strength of either mechanism. Positive covariance in abundance or biomass is more common than negative covariance, but negative covariance is more common within functional groups (Table 1). Resource abundance likely is an important determinant of the density of shrews in an ensemble, but it does not appear to differentially affect particular species. Rather, abundances of all species increase with increasing resource availability, maintaining similar relative abundances and unchanged structure in the ensemble, a fact that may reflect the tendency of shrews to be foraging generalists. The structure of Congolese shrew ensembles is a consequence of either stochastic processes or a balance of competitive interactions and responses to variation in resource abundance.

Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Morphological measurements used to define functional diversity.

Supplementary Data SD2.—Ecomorphological traits for species of shrew.

Supplementary Data SD3.—Relative abundance as a percentage per species of each ensemble.

Supplementary Data SD4.—Relative biomass as a percentage per species of each ensemble.

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Author contributions

FVdP and MRW conceived of the research idea; FVdP collected and curated the data; FVdP and SJP conducted statistical analyses; FVdP, MRW, and SJP wrote the manuscript; EV and HL managed the research project; all authors contributed to interpretation of results and edited the manuscript.

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Conflict of interest

None declared.

Data availability

All data are available at http://projects.biodiversity.be/afric-anmammalia. In addition, all data occur in associated online Supplementary Data files.

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