Macroeconomics of local insect communities

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Abstract — The inter-relationships between animal body weight, range size, species richness and abundance are currently the basis of macroecology. Using 41,099 insects sampled from 31 Acacia tree canopies in north-east Tanzania, we first documented the basic macroecological patterns. The relationship between body weight and both species richness and abundance was polygonal with the highest insect species richness and abundance occurring at intermediate body weights. Across individual tree communities, the most statistically robust relationships were found between range size, abundance and species richness and they were all linear. In a second part, we focused on the positive abundance-range size relationship and we could test predictions of six of the eight proposed hypotheses to explain this widely documented pattern of community structure. The relationship is most likely explained by the metapopulation hypothesis stating that with more patches being occupied, local abundance in a given patch increases due to a higher rate of immigration from nearby patches. In addition, we found high slopes for the species-area relationship, typical of island systems and thus it seems reasonable to characterise Acacia trees in the savannah as habitat islands for insects. © 2000 Éditions scientifiques et médicales Elsevier SAS

1. INTRODUCTION

Macroeconomics can be described as the study of emergent patterns of assemblages of species distributed over geographical spatial scales and evolutionary time scales [11, 21, 36]. These patterns are frequently characterised by four variables: body weight, range size, species richness and abundance [2-6, 12-16, 18-20, 22-25, 28, 34, 37, 44, 45, 52, 53, 58, 59]. Among the possible combinations of these variables, a central role is played by the three interspecific relationships between abundance, range size and body size (see [21] and references therein) and enormous progress has been made concerning bivariate relationships. Over 300 interspecific species-body size, 500 interspecific abundance-body size and well over 100 abundance-range size relationships have been published (however, only around 25 studies reported on the range size-body size relationship, see [21]). These relationships are not only of interest to macroecologists but a deeper understanding of the responsible mechanisms would greatly enhance our understanding of the causes of rarity and commonness and thus are a helpful tool for all conservationists alike [21]. However, there is an enormous bias in the publication record. Over 75% of abundance-range size reports come from North America and Europe and over 75% of abundance-body size reports focused on vertebrates only so that the regions and taxa of high species richness are currently very much understudied. Thus, although documenting these patterns can be regarded as ‘stamp-collecting’ [21], we cannot be sure that the reported patterns also apply in the tropics and to more speciose taxa such as insects.

The widespread use of knockdown methods and other techniques to collect arthropods has resulted in a number of large data sets which have been analysed with regard to the relationships between body weight, species richness and abundance [1, 48, 50, 54, 56]. These data are very suitable for analysis, since they
cover a wide range of taxonomic orders, body types and ecological niches [47, 56] and can provide insights into community ecology. Range size, however, has rarely been included since most studies were conducted at one or a few sites only so that no data on local range sizes could be collected (but see [54] for an example concerning insects).

Here we analyse the local insect communities associated with Acacia tree canopies in Mkomazi Game Reserve, north-east Tanzania, with regard to the relationships between body weight, range size, species richness (total number of species) and abundance. First, we look at the entire community where all samples were combined. Second, we divide the community into body weight classes and explore the inter-relationships between the four variables across body weight classes, because body weight is commonly regarded as the variable with the biggest predictive power in macroecology [2]. Third, we compare communities across trees and focus on one variable combination, the abundance-range size relationship. This, very often positive, relationship is of greatest importance in times of great biodiversity loss since it ultimately asks why certain species have a low extinction risk (widespread and abundant) while others exhibit a high risk (localised and rare). Eight different hypotheses have been proposed to account for the relationship [24]. They are not mutually exclusive [21] and a test of their predictions using a single assemblage has rarely been made. Two regard the relationship as artefactual (sampling artefact [10] and artefact of phylogeny [31]) and six put forward a biological explanation (range position [8], breadth of resource usage [10], resource availability [29], habitat selection [51], metapopulation [29] and vital rates [33]). We do not test two hypotheses (range position and vital rates) since they require either large scale geographical range size data or birth and death rates. Sadly, there is no sufficient data for Afrotropical insects. Instead, we focus on the two artefactual as well as four biological hypotheses (breath of resource usage, resource availability, habitat selection and metapopulation) because they can be reasonably tested using regional scale data. We explicitly test their predictions in order to see which is most likely to explain the relationship in our data.

2. MATERIALS AND METHODS

Thirty-one Acacia trees of six species (A. ethaica, mellifera, nilotica, reficiens, senegal, tortilis) were sampled in Mkomazi Game Reserve, north-east Tanzania, between 30 December 1995 and 18 January 1996 at nine localities between 50 m and 31 km apart (for a detailed basic data breakdown, see [40]). The area is a semi-arid savannah with a pronounced dry season and mean rainfall between 300 and 900 mm. Insects were sampled using the mist-blowing technique [39-41] using a fast-acting insecticide (Pybuthrin 216). Insects were collected in 1-m² funnel-shaped trays, suspended between stakes, over a standard drop-time of 1 h. The material was identified to family level by specialists and then morphotyped (RTU, in the following species). Body length was used to calculate dry biomass, using an allometric formula given by Moran and Southwood [47]. To avoid overestimation of species richness, larvae were excluded from the analysis, so that underestimation is more likely. The lightest species was taken as the starting point and other species were grouped into body weight octaves which represent a body weight doubling. For each tree, geometric mean body weight of all species present, mean range size (proportion of trees where a species was found averaged for all species on a tree), species richness (total number of species found) and abundance (ind-m⁻²) were calculated. Species abundances include only those trees where a species occurred. We used partial correlation analysis with \( P < 0.05 \) as a significance threshold to see which variables were most likely significantly correlated with each other. Because of sampling errors, relationships cannot be analysed using ordinary least square regression which is considered to be unreliable [27, 46]. Instead, the reduced major axis method is strongly recommended [27, 46] and was applied. We normalised the binomial distributed range size variable by arcsine-transformation and statistical analysis was done in SPSS and STATISTICA.

3. RESULTS

3.1. Macroecological patterns in the entire community

We obtained 41 099 insects of 133 families and 492 species, which is estimated to be around 77 % of the true richness of the 31 trees (for a detailed taxonomic breakdown of the current data set, see [39]). The inter-relationships between body weight, abundance and range size (figure 1) indicate that body weight has weak negative relationships with abundance (figure 1A) and range size (figure 1B). The
abundance-range size relationship, in contrast, was strong and positive (figure 1C). The relationship between body weight and abundance was weakly significant when range size was controlled for (partial $r = -0.092$, df = 489, $P = 0.041$) while both the body weight-range size and abundance-range size relationships were highly significant (partial $r = -0.171$, df = 489, $P < 0.0001$, controlling for abundance and partial $r = 0.682$, df = 489, $P < 0.0001$, controlling for body weight, respectively). Sampling inevitably introduces errors, so we performed a control analysis where only those species were included of which at least twenty individuals were sampled ($n = 133$ species or 27% of the total). Body weight was not significantly partially correlated with abundance ($r = -0.045$, df = 129, $P = 0.611$) but negatively with range size ($r = -0.275$, df = 129, $P < 0.001$). The abundance-range size relationship was still highly significant and positive (figure 1D, $r = 0.482$, df = 129, $P < 0.0001$).

After grouping species into body weight classes, body weight and both species richness and abundance had a non-linear relationship with peaks at intermediate body weights (figure 2A, B). The same was found for the four main insect orders (Hemiptera, Coleoptera, Diptera and Hymenoptera) for species richness and abundance with the exception of Diptera, where the relationship between abundance and body weight was linear (see [38]). To see which other inter-relationships were strongest, partial correlation analysis was performed and the results are given in table I. Body weight was not significantly correlated with any of the other three variables while these were strongly inter-correlated.
3.2. Macroecological patterns across trees

In this section, the 31 tree communities will be compared. Differences in the four variables might be expected between different tree species and sampling localities due to host-specificity or spatial heterogeneity. However, two-way ANOVA showed that this was not the case (table II). None of the four variables exhibited significant differences between tree species, sampling localities and there was also no significant interaction of the two factors. In addition, host specificity does not play an important role, indicated by cluster analysis (see [40]). It is therefore reasonable to look for correlations among the variables across the whole number of trees sampled. Results of partial correlation analysis are shown in table III and were similar to the results of the body weight classes analysis. Geometric mean body weight was not correlated with species richness and abundance but negatively with range size. The inter-relationships between range size, species richness and abundance were all highly significant. Lack of significant interactions between body weight and both species richness and abundance was not caused by a non-linear relationship. Thus, mean body weight was not a significant predictor across trees except for range size which decreased with body weight.

Table I. Partial correlations between body weight classes (log₂), mean range size, species richness and abundance (df = 15). The two left-out variables are controlled for, P-values are in parenthesis.

<table>
<thead>
<tr>
<th></th>
<th>Mean range size</th>
<th>Species richness</th>
<th>Abundance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body weight</td>
<td>-0.129 (0.621)</td>
<td>0.282 (0.272)</td>
<td>-0.303 (0.237)</td>
</tr>
<tr>
<td>Mean range size</td>
<td>-0.745 (0.001)</td>
<td>0.827 (0.001)</td>
<td></td>
</tr>
<tr>
<td>Species richness</td>
<td></td>
<td>0.939 (0.001)</td>
<td></td>
</tr>
</tbody>
</table>

3.3. Abundance-range size relationship

In this section, we test predictions of the six selected hypotheses in order to see which is most likely for our data.

1) Sampling artefact. Rare species, although potentially widespread, are rarely sampled and their ranges are consequently underestimated. This is unlikely to be the causal factor for our data for two reasons. First, it can be estimated that a good proportion (77 %) of the true species richness has been sampled. Second and more important, restricting the analysis to those species for which at least twenty individuals were sampled also provides a positive relationship (figure 1D); even if only species for which at least fifty individuals were sampled (n = 68 species or 13.8 % of the total) are included, the positive relationship still holds (r = 0.395, df = 66, P < 0.01). Thus underestimation of range size due to sampling bias alone cannot account for the relationship in our data. In the following, we use the restricted data set (> 20 ind. sampled) for hypotheses testing to minimise the effect of sampling bias on the outcome of the tests.

2) Artefact of phylogeny. Because of their phylogenetic relatedness, species are not independent data points. If taxonomic units differ significantly in range size or abundance, a cross-species correlation might be significant because of phylogeny and not ecology. There was no significant difference between the fourteen insect orders in mean range size ($F_{13,119} = 1.234$, $P = 0.264$) but there was one in abundance ($F_{13,119} = 5.377$, $P < 0.0001$). As an explicit, although
admittedly crude test, we used independent contrast analysis at the order level based on a phylogenetic tree [9]. Contrasts in range size were positively correlated with contrasts in abundance (figure 3A, $r = 0.751$, $df = 11$, $P < 0.01$). The relationship is thus unlikely to be a phylogenetic artefact which has been found in other studies [20, 23, 25, 49, 54].

3) Breadth of resource usage. Wide ranging species have higher densities because they use a wider range of resources compared to narrow ranging species which should be more specialised. This hypothesis makes three predictions of which one can be tested here, although on a rather crude level. Species occupying fewer and fewer sites should have narrower and narrower niche breadths [24]. To obtain an estimate of niche breadth, we calculated on how many different tree species an insect species was present, assuming that different tree species reflect in some way niche breadth. We only used the restricted data set (> 20 ind. sampled) because a species sampled only once is constrained to be found on one tree. For the restricted data set, this constraint does not play a major role. A positive correlation between this niche breadth measure and range size and, more important, abundance, would support the prediction. Indeed there were highly significant positive correlations between the niche breadth measure and both range size ($r = 0.726$, $df = 131$, $P < 0.0001$) and abundance ($r = 0.209$, $df = 131$, $P = 0.016$). At a crude level, there is support for this hypothesis in our data.

Table III. Partial correlations between geometric mean body weight, mean range size, species richness and abundance across the 31 trees studied ($df = 26$). The two left-out variables and sample size were controlled for, $P$-values are in parenthesis.

<table>
<thead>
<tr>
<th></th>
<th>Range size</th>
<th>Species richness</th>
<th>Abundance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body weight</td>
<td>-0.439 (0.019)</td>
<td>-0.104 (0.599)</td>
<td>0.239 (0.221)</td>
</tr>
<tr>
<td>Range size</td>
<td>-0.772 (0.001)</td>
<td>0.394 (0.039)</td>
<td></td>
</tr>
<tr>
<td>Species richness</td>
<td></td>
<td>0.665 (0.001)</td>
<td></td>
</tr>
</tbody>
</table>

Figure 3. Relationship between independent contrasts in range size and abundance for the fourteen insect orders present in this study (A); regression was forced through the origin [17] but is still significant ($R^2 = 0.433$, $df = 11$, $P < 0.05$). Relationship between range size and abundance for those species for which at least twenty individuals were sampled in comparison with species of Diptera and Hymenoptera for which at least twenty individuals were sampled (B). Slopes are 41.4 for the entire community, 58.8 for Diptera and 54.6 for Hymenoptera.
4) Resource availability. Wide ranging species are abundant because they use abundant and widespread resources. This hypothesis makes two predictions amenable for testing. First, species that share a common resource base should not show a positive abundance-range size relationship. We used the phytophagous sapsuckers in the order Hemiptera with sampling > 20 individuals to test this because their food niche can be considered to be very common on Acacia trees. They should have, at least, a much weaker abundance-range size relationship compared to the entire community since they comprise a clearly defined ecological guild within a clearly defined taxonomic unit. However, the relationship is stronger compared to the entire community ($b = 0.024$ and $r = 0.515$ for the community and $b = 0.022$ and $r = 0.780$ for hemipteran sapsuckers). Second, resource specialists can be abundant and widespread. Support would be no positive relation between niche breadth and range size and abundance. Since we found positive correlations, this predictions is not supported either.

5) Habitat selection. Density-dependent habitat selection produces the abundance-range size relationship. A further development [43] leads to a testable prediction which is that the slope of the abundance-range size relationship should be proportional to the number of resources. We tested this by using tree species as surrogates for resources; slopes should be lower for the species set found on one tree species compared to those found on more or all tree species. This is not the case for the restricted data set. Species found on one tree species exhibit an abundance-range size relationship with a slope of $-0.076$, species found on two tree species have a slope of $0.047$, for three tree species the slope is $-0.094$, for four tree species it is $-0.060$, for five it is $0.030$ and species found on all six tree species have a slope of $0.029$. The proposed proportionality thus does not hold for our data.

6) Metapopulation hypothesis. The rescue effect proposes that immigration decreases the probability of local population extinction and that the immigration rate for a given habitat increases with the proportion of habitats occupied. Among five predictions of this hypothesis, two can be tested. First, there should be a positive abundance-range size relationship even where there is no difference in niche breadth. In line with this prediction, there was a highly significant correlation between abundance and range size (restricting the analysis to species with sampling > 20 individuals which were found on all trees $r = 0.797$, $df = 25$, $P < 0.0001$). Second, species with high dispersal rates should have a wider range size for a given abundance compared to less dispersive species. Figure 3B shows the abundance-range size relationship for the community and two more dispersive orders such as Diptera and Hymenoptera using the restricted data set. In order to quantify differences, we used the reduced major axis slope for the entire community and compared it with the ones of Diptera and Hymenoptera (figure 3B). For a given abundance of $1.0 \text{ ind}\cdot m^{-2}$, range size is $53.4\%$ for the entire community, $65.3\%$ for Diptera and $79.3\%$ for Hymenoptera. For Hymenoptera, the value is significantly larger compared to the community (Fischer’s exact test: $t = 2.560$, $df = \infty$, $P < 0.02$) while there is a trend for Diptera ($t = 1.805$, $df = \infty$, $P < 0.10$). The metapopulation hypothesis is thus well supported by our data.

4. DISCUSSION

Our data set is one of the first examples where Afrotropical insect data was usable for testing and distinguishing between macroecological hypotheses (see [47] for another such example, and [54] for a temperate region). It is also one of the largest samples ever collected from a tropical savannah habitat. Therefore the taxonomic broadness as well as the large sample size makes it suitable for the kind of analysis we have performed here. However, it has been clearly emphasised that broad generalisations from the analysis of a single assemblage should be avoided [21]. Here we just want to point out the differences and similarities to other studies.

The results are in line with the reported patterns in macroecology in some aspects but not in others. Non-linear relationships between body weight and both species richness and abundance are common within taxa [3, 4, 7, 12, 14, 16, 20, 35, 48, 56]. Although RTUs are not synonymous with species, it is unlikely that errors during the morphotyping process are responsible for this relationship. The $23\%$ of RTUs estimated to be absent in the samples might constitute a biased subset [2], possibly towards smaller organisms, but this would not change the bell-shaped patterns reported here qualitatively.

The polygonal negative relationship between body weight and abundance is frequently reported from local studies [5] while regional or continental studies mainly reported linear negative relationships. The slope of $-0.5$ is in good agreement with Blackburn and Gaston’s findings [5] who reported a mean slope of $-0.51$ from 291 studies and the results of Griffiths [27] who proposed a broad general negative relationship with a slope around $-1$.

In contrast to most other studies, the relationship between body weight and range size was linear and negative instead of positive. It has been pointed
out [19] that local studies more frequently report negative relationships and that these might involve artefacts, so the result should be treated with caution. The strongest relationships, however, in the entire community and across trees, are those between range size, species richness and abundance which has been found elsewhere [20, 49].

With regard to the abundance-range size relationship, among the six hypotheses for which predictions could be tested, the metapopulation hypothesis is best supported and there is also some support for the breadth of resource usage hypothesis. The other four (sampling artefact, phylogeny, resource availability, habitat selection) are unlikely to explain the relationship for our data. It has been shown [30] that a positive relationship can be expected a priori on the basis of random distribution of species. Nevertheless Gaston et al. [26] point out that it is difficult to predict a priori what form the relationship should take and that random draw alone cannot account for it.

The metapopulation hypothesis makes intuitive sense for this habitat where scattered trees in the savannah might be habitat islands. In addition, species-area relationships (area measured as sampling area in m²) in the community and for the four most speciose taxa show exponents around 0.35 [39], typical of island systems [28, 42, 55]. But slopes are also inflated by sampling errors [32], so their high exponents are questionable. However, the support for the metapopulation hypothesis explaining the abundance-range size relationship and the slopes of the species-area curves are two pieces of evidence that trees in the savannah can be characterized as habitat islands for insects (but see [57]).

Acknowledgments

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