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Species richness correlations between taxa calculated from species-area relationships

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ABSTRACT

Predicting the species richness of certain taxa from the richness of others could be of great value in biodiversity conservation. If we know how the species richness of groups of organisms correlates to each other under different circumstances, inventories of only a few well-known taxa could be enough to establish the biodiversity values of different areas. In this master thesis I have examined the richness correlations between taxa from species-area relationships extracted from the literature to evaluate the possibilities of this approach.

Calculations of the pairwise correlation between the residuals of the species-area relationships of different taxa found in the literature resulted in 503 correlation coefficients. Of the 79 taxa covered, the most frequently examined groups (several taxa included) were plants > butterflies > true bugs > birds > mammals. Only 157 of the 503 correlations were significant. An average effect size of 0.373 (95 % CL = 0.059) indicates positive but usually weak correlations between taxa in the very heterogeneous dataset. The dataset was divided into a number of categories (according to spatial scale, taxonomic distance, trophic position, biotope and climatic region) to investigate some hypotheses, for example (1) that richness of closely related taxa are likely to be more correlated than distantly related taxa, and (2) that correlations between plants and animals are higher than correlations among plants or among animal groups. Between families – within order comparisons had significantly higher correlation than comparisons in all other taxonomical classes except between kingdoms. These results were in agreement with my hypotheses concerning taxonomic distance and trophic position.

No universal indicator taxon has been found to predict the species richness of other taxa. With more careful studies in certain biotopes and at appropriate spatial scale perhaps good indicator groups can be discovered. These are unlikely to be universal and it is probable that indicator taxa are only useful at regional scales.

Keywords: Species richness correlations, meta-analysis, species-area relationships, taxonomic distance, biodiversity

SAMMANFATTNING

Förutsägelser av artrikedom hos vissa organismgrupper från diversiteten hos andra grupper skulle vara till stor hjälp i naturvårdsarbetet. Om man vet hur artrikedomen hos organismgrupper korrelerar med varandra under olika betingelser, kan man genom att bara inventera ett fåtal taxa bedöma ett områdes biodiversitetsvärdet. I mitt examensarbete har jag undersökt diversitets-korrelationerna mellan taxa från art-areakurvor hämtade i litteraturen för att kunna utvärdera möjligheterna av denna infallsvinkel som hjälp i naturvårdsarbetet.

Genom att räkna ut den parvisa korrelationen mellan residualerna från art-areakurvorna hos olika taxa i litteraturen fick jag 503 korrelationskoefficienter. Av de 79 inbegripna taxa var de vanligaste undersökta grupperna (flera taxa inkluderade) växter > fjärilar > skinnbaggar > fåglar > däggdjur. Endast 157 av 503 korrelationer var signifikanta. En medeleffektstorlek på 0,373 (95 % konfidensintervall = 0,314 - 0,432) indikerar positiva men svaga korrelationer mellan taxa i det väldigt heterogena datamaterialet. Materialet delades upp i ett antal kategorier (enligt rumslig skala, taxonomisk distans, trofisk position, biotop och klimatisk region) för att undersöka några hypoteser, till exempel (1) att diversitetskorrelationer mellan nära besläktade

taxa är högre än mellan avlägset besläktade taxa, och (2) att korrelationer mellan växter och djur är högre än mellan växter eller mellan djurgrupper. Korrelationer för jämförelser mellan familjer – inom ordning var signifikant högre än för jämförelser i alla andra taxonomiska klasser utom för jämförelser mellan riken. Dessa resultat överensstämde med mina hypoteser om taxonomisk distans och trofisk position.

Någon universell indikatorgrupp som förutsäger artdiversiteten hos andra grupper har inte hittats. Kanske kan lämpliga indikatorgrupper upptäckas med mer grundliga studier i särskilda biotoper och på passande rumslig skala. Dessa kommer sannolikt inte att vara universella och det är troligt att indikatortaxa bara är användbara på regional skala.

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INTRODUCTION

It has been suggested that the species richness of well-studied taxa possibly could predict the diversity of other less studied taxa. This would be of great aid to conservationists, since mapping of all taxa would not be needed to estimate the biodiversity values of an area (Prendergast 1997). It would also facilitate the prioritisation among areas that have been proposed as possible reserves.

It is known that there is a broad positive association between plants and animals at the global scale, since both groups increase into the tropics (Hawkins et al. 2003). Evidence of correlation at smaller, regional scale is more limited, whereas at the local scale diversity correlations between plants and animals have been found in several studies (e.g. Haddad et al. 2001; Knops et al. 1999; Siemann et al. 1998). There are many reasons for the correlation between plants and animals, but the most obvious is that a greater diversity of resources should support a greater diversity of consumers. Many studies also show a correlation between other organism groups, but it is often difficult to know whether the connection is causal or due to similar responses to environmental factors (Hawkins et al. 2003). There are several explanations for why the species richness in different taxa can be connected; random coincidence, interactions between taxa, similar response to common biotic and abiotic factors, and response to different environmental factors that are spatially covariant (Wolters et al. 2006).

There are also studies that show low correlation between diversity in different taxa. Lawton et al. (1998) showed that species richness in several organism groups generally decreases with increasing disturbance in the tropics, but that none of the studied organism groups could function as a good indicator taxon. In a study in Great Britain, Prendergast et al. (1993) showed that species-rich areas ("hotspots") of different taxa rarely coincide.

Wolters et al. (2006) performed a metaanalysis of 152 correlation coefficients between different taxa in the recent literature and found that the overall average correlation coefficient was 0.374. This indicated positive but weak correlations between taxa in the very heterogeneous data set. They found a marked lack of negative correlations (only 5 of 152), which suggests that negative correlations are less likely to be published. This might be due to a biased selection of organism groups (selection of taxa that are anticipated to be correlated), which would result in a large proportion of positive correlation coefficients. It could also be caused by negative correlations being less likely to be published.

Species-area relationships can be used to calculate species richness correlations that would not be subject to the bias against negative correlations discussed above. This is done by correlating the residuals from the species-area relationships of two groups studied at the same set of islands or plots. However, there can be problems when comparing taxa responding to different factors at different spatial scales. The correlation coefficients from species-area relationships are advantageous compared to using published correlation coefficients because published species-area relationships are probably not biased towards positive or significant correlations, which published correlation coefficients can be, since the latter are calculated from groups selected for their putative indicator qualities.

A major hypothesis to be examined is that closely related taxa are more correlated than taxa further apart taxonomically. Since related taxa have a similar evolutionary history and may respond similarly to environmental factors, their residuals from the species-area relationships might coincide, which would yield a high correlation coefficient. Another hypothesis, which

was mentioned previously, concerns that plants and animals are expected to be more correlated than plants-plants and animals-animals. Other hypotheses could be formulated concerning the spatial scales used for correlations. However, making predictions about relationships between correlations at different spatial scales is very difficult. One might expect smaller organisms to have higher correlations on smaller spatial scales and the opposite for bigger organisms, but it all depends on what factors different groups respond to, and what spatial scales these factors act on.

The purpose of this master thesis is to investigate if there is a positive correlation between the species richness of different taxa, and if in that case the connection is stronger between closely related taxa than distantly related taxa or stronger between plants and animals than within kingdom comparisons.

MATERIALS AND METHODS

To examine the correlations between taxa after accounting for area (i.e. the species-area relation), I used the following procedure:

1. Data was collected from the literature. All publications with data on species number and area with a minimum of two taxa from at least five plots (islands) were selected.
2. Regressions between log species number and log area were calculated for each group (taxon) in a publication.
3. The residuals from the regression line were taken for each group and the pair-wise correlation between the residuals was calculated for all combinations of pairs of taxa.
4. The dataset was subdivided into different categories; e.g. taxonomic distance classes and trophic position, to be able to further examine the patterns and to test some *a priori* hypotheses; (1) that richness of closely related taxa are likely to be more correlated than distantly related taxa, and (2) that correlations between plants and animals are higher than correlations among plants or among animal groups.
5. All correlations were included in a meta-analysis that examined if the overall correlation mean was positive or negative, and whether it was significant.
6. Since there was significant heterogeneity in the dataset, the data was divided into the subsets (see point 4), which were examined according to point 5.

Data sources and definitions

I searched the databases available at the Swedish University of Agricultural Sciences (SLU, Sweden) for the following key-words (in different combinations): species-area, richness, area, diversity, indicator taxa, species number, species lists, inventories and correlations. I also reviewed all issues from 1980 to 2006 of the Journal of Biogeography as well as obtained a number of older articles from my supervisor's library. The articles containing data on species number and area with a minimum of two taxa from at least five plots (islands) were selected. This procedure yielded 20 papers providing information on 503 richness correlations between taxa, and 46 richness correlations between a single taxa and the total number of species in a study from 3 of the papers. My focus has been on terrestrial systems since the information on limnological and marine systems seemed comparatively poor. The literature search was terminated on the 31st of March 2006.

To be able to understand what factors that might influence the sign and magnitude of richness correlations, the data was subdivided into a number of different categories as follows:

The pairs of taxa were allocated to six classes of taxonomic distance based on the categories genus, family, order, class, phylum and kingdom respectively (fig 1).

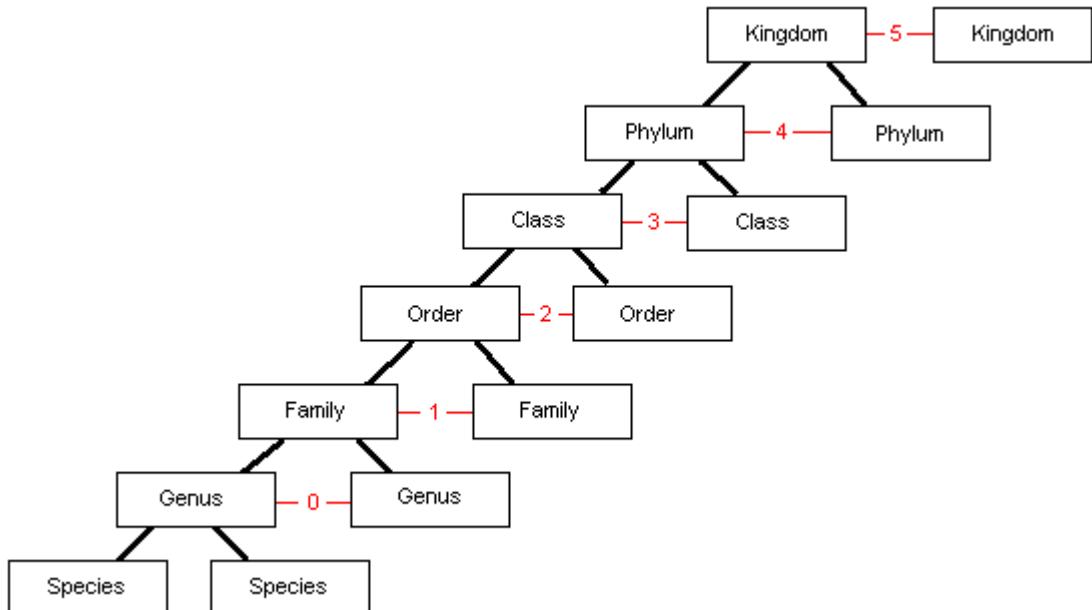


Figure 1. Schematic picture of the taxonomic distance classes. The numbers 0-5 indicate the classes.

Correlations between two genera belonging to the same family formed class 0. However, there were no pairs of taxa in class 0 in this study. The correlations between two families of the same order were allocated to class 1 (e.g. the butterfly families *Danainae* and *Morphinae* of the order *Nymphalidae*), correlations between two orders of the same taxonomic class belonged to class 2 (e.g. correlations between two families of different plant orders *Rosales* and *Fagales* of the class *Spermatopsida*) and so on for class (class 3), phylum (class 4) and kingdom (class 5). The correlations were also divided into three classes depending on trophic position: autotrophic vs. autotrophic (plants, class 1), autotrophic vs. heterotrophic (plants vs. animals, class 2) and heterotrophic vs. heterotrophic (animals, class 3). The position in climatic belts (temperate, tropical, arctic and global including all belts) and macro habitat type (forest, desert etc.) was also noted for all richness correlations. When several climatic belts or habitat types were covered in a study it was termed “multi”.

The dataset was also divided into three area classes (table 1), depending on at which spatial scale the species-area relation was estimated. The spatial scales varied greatly among the studies and the mean areas ranged from 0.023 to 1 570 000 km². The classes were set at natural breaks in the distribution of area means of the 20 references.

Table 1: Area classification

| Area class (x) | Area (km ²) |
|----------------|-------------------------|
| 1 | 0 < x < 60 |
| 2 | 60 < x < 6000 |
| 3 | 6000 < x < 1600000 |

Data treatments and calculations

For each taxon the regression between log transformed species number (y) and log transformed area (x) and the residuals (distance from each data point to the regression line) were calculated (fig 2) using MS Excel procedures (Microsoft Excel 2000). For some taxa the species-area relationship (the regression) was insignificant and thus correction for area was not necessary, but for consistency all taxa were treated identically and the regression and residuals were calculated for all of them. The correlation between two taxa was estimated by calculating the pairwise correlations between the residuals for the two taxa. The correlation shows how well the datapoints (from different taxa) coincide in relation to each other and to the regression line. Since points for different taxa have the same x-axis values (log area), the comparison is between the y-axis values (log species number), that is the distance from the regression line (the residuals). A point located below the regression line yields a negative residual and one above the line yields a positive residual. For example, two positive residuals of similar magnitude in two taxa means that both groups have relatively high species richness on that island (plot), and if this pattern holds across all islands (high/high or low/low richness) it yields a high positive correlation. An example of this can be seen in figure 2 where the correlation coefficient between the residuals of vascular plants and birds is 0.95 (Lack, 1969).

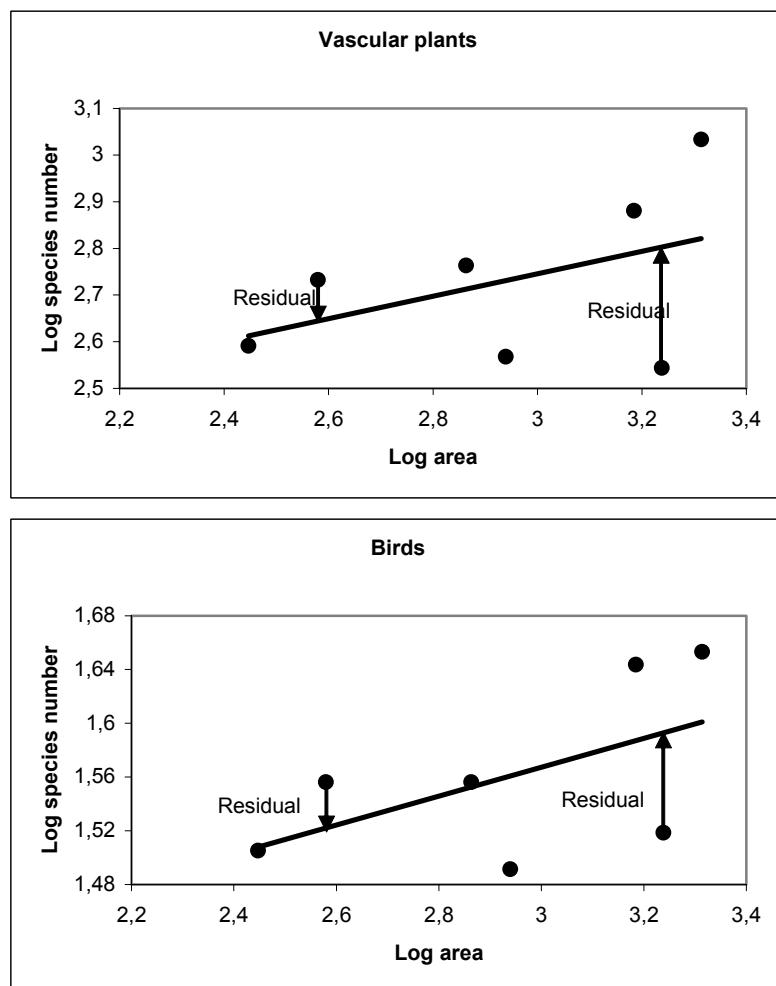


Figure 2: Species-area relationship for vascular plants (above) and birds (below). The distance from a data point to the regression line is called residual. Data on vascular plants and birds on the Canary Islands from Lack (1969).

Deviations from the data treatments

The above procedure of data treatments and calculations was followed in all cases where it was possible. However, in some cases deviations were necessary. In Kitchener et al. (1980 a, b) the data on area for some of the same islands off the coast of Australia differed between the two articles and in those cases I used the data from Kitchener et al. (1980a). In Beccaloni et al. (1994) three of the plot areas were assigned as “less than” (<) a certain value since the areas were assumed to be smaller than what the sources stated. However, since no other values of the areas were mentioned, I used these areas in spite of their possible uncertainty. In Chown et al. (1998) there were values for indigenous species, introduced species and total number of species for some of the organism groups. I used the values for total species number, except for seabirds where only values for indigenous species existed and mammals where only values for introduced species existed. In Connor et al. (1978) there were no data on area of the Galapagos Islands, so sources on the Internet were used. For Galapagos islands Darwin, Marchena, Pinta, Pinzon and Wolf the internet page of Galasam Galapagos tours (www.galapagos-seniors.com) was used, and for islands Espanola, Fernandina, Genovesa, Isabela, Rabida, San Cristobal, San Salvador (Santiago), Santa Cruz, Santa Fe and Santa Maria (Floreana) the internet page of Galapagos yachts (www.galapagosyachts.com) was used. In Hansson (1997) there were data for both common and rare species but I used the total species number. In Ahlén et al. (1982) the data on species numbers for birds were divided into several categories depending on sampling methods. I chose the species numbers from the category “probable breeding” for birds. In Söderström et al. (2001, unpublished data) birds were sampled in a bigger area than were the other organisms. For consistency I needed to use the same set of area data for all organism groups so I chose the bigger area since this was the only set with values of area for all plots. When data for both sampling years 1996 and 1997 were available I used, as did the authors, data from 1997. In Wright (1981) there were data from the California Channel Islands for the organism groups amphibians, reptiles, nonvolant mammals and birds. In Moody (2000) I found data for plants also from the California Channel Islands. Hence I could calculate the correlation coefficients between all these five taxa using data on island area from Wright (1981).

Meta-analysis

All correlation coefficients were included in a meta-analysis of correlations between taxa (largely following Wolters et al., 2006). Meta-analysis is a method of analysing and synthesising the results of several independent studies examining the same question. The statistical procedures of a meta-analysis account for the fact that studies are not equally reliable (Wolters et al. 2006), in the present case in terms of the number of islands (plots) included in each correlation.

The average sizes of the correlations in the dataset and in the different subsets were examined and groups of taxa that are likely to interact strongly (like autotrophs and heterotrophs) were compared to groups of taxa that are less likely to interact.

The equation $z_i = 0,5 * (\ln[(1+r_i)/(1-r_i)])$ was used to transform all correlation coefficients r_i to z-transformed correlations. By then multiplying z_i with its conditional variance ($v_i = 1/(n_i-3)$), greater weights were assigned to studies with larger sample sizes (n) since v_i is inversely related to n (Cooper and Hedges, 1994). The sample sizes for individual correlations varied between 4 and 37. The studies with small sample sizes are less reliable than the ones with greater sample sizes; hence they should be weighed accordingly.

The estimates of individual z_i and v_i were then included in a fixed effects model and a random effects model. The models investigated if the overall mean of the weighted correlation

coefficients differed from 0 (no correlation). If the 95 % confidence limits did not include 0, the mean correlation was regarded as significant. When different subsets of the data were compared, two means were considered to differ significantly if there was no overlap between the confidence limits. The results were then transformed back to correlation coefficients (r) and confidence limits for the purpose of interpretation and illustration (fig 5).

For the fixed effects model a weighted average effect size and a homogeneity test statistic Q was calculated. If Q was significant ($Q > \chi^2$ for $df=n-1$), which was commonly the case (all but two of the subsets, which had $n = 2$ and $n = 10$ respectively) in my study, effect sizes were heterogeneous and differed among the studies meaning that there was no common effect size that all studies estimated. Since Q was almost always significant and no common effect size seemed to exist, the random effects model seemed to be the most appropriate model to use and was hence used to estimate the effect sizes in all cases.

I subdivided the studies according to area class, taxonomic distance, trophic position, climatic belt, and biotope. If the studies in these subdivisions were still heterogeneous (significant Q), factors not included in the study contribute to the variation among correlations.

I used the Excel spreadsheets with meta-analysis calculations developed by Wolters et al. (2006), which had been checked previously with data in Cooper and Hedges (1994; J. Bengtsson pers. comm.).

RESULTS

Data structure and frequency distribution

The 503 richness correlations covered 79 taxa at different taxonomic levels, with between 1 and 35 correlations per taxa (appendix 1). The 20 references provided between 1 and 190 correlations each. The most frequently examined groups (several taxa included) were plants with 410 correlations (41 % of 1006 correlations = 503 correlations with two taxa in each), *Lepidoptera* (20 %), *Heteroptera* (13 %), birds (4 %, including sea birds and land birds) and mammals (3 % including nonvolant mammals, rodents and bats). The frequency distribution of correlations among taxonomic distance classes showed a bias towards those between more closely related taxa (except class 0 – different genera in the same family) with 0, 163, 196, 92, 22 and 30 correlation coefficients in classes 0-5 respectively.

The area classes included 6 (class 1), 10 (class 2) and 7 (class 3) references respectively, and 95, 43 and 365 correlations in classes 1-3 respectively. To trophic position 1, 190 correlations (38 %) were allocated, 30 (6 %) were allocated to trophic position 2 and 283 (56 %) to trophic position 3. Most studies were performed in a multitude of biotopes (77 %), 20 % in forest, 2 % in semi-natural pastures, and less than 1 % in other habitats. Sixty-three percent of the studies were made in tropical areas, 23.5 % in temperate areas and 13.5 % in more than one climatic belt. The distributions of correlations in the different subsets are illustrated in appendix 2 with positive significant, negative significant and non-significant positive and negative correlations in each category.

Out of 503 richness correlations, 137 (27 %) were positive and significant, 220 (44 %) were positive but insignificant, 20 (4 %) were negative and significant and 126 (25 %) were negative but insignificant (appendix 2 and fig 3).

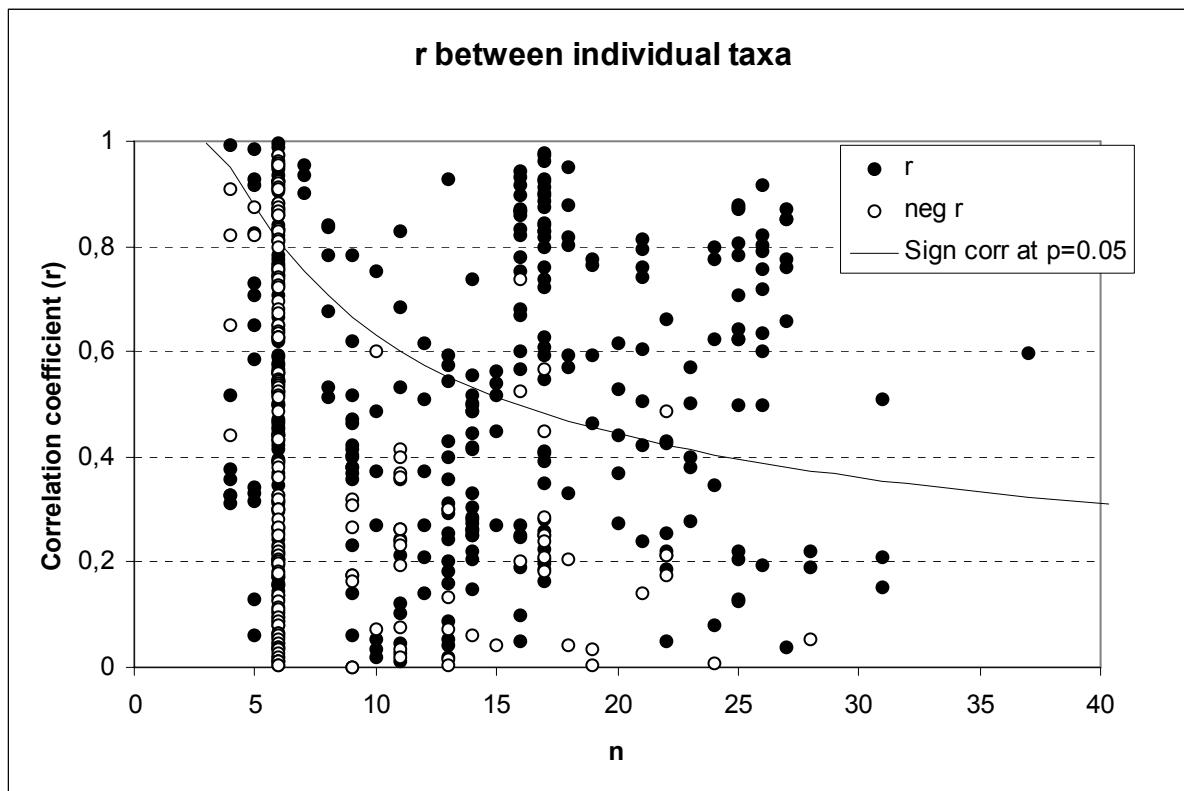


Figure 3. The distribution of correlation coefficients (r) and sample sizes (n) in the data set. The line indicates the values of r that are significant at $p = 0.05$, the points above the line being significant. Open dots indicate negative correlations.

Data structure and frequency distribution in total species vs. individual taxa

Comparison between total number of species in a group and the individual taxa in that group, such as total invertebrates compared to *Collembola*, yielded 46 richness correlations of which 20 were significant, 35 (18 significant) were positive and 11 (2 significant) were negative (fig 4).

This dataset only included correlations from taxonomic distance classes 1 and 3 with 14 and 32 correlation coefficients respectively. The area classes 1 and 3 were represented with 12 and 34 correlations respectively. Twenty correlations were allocated to trophic position 1 and 26 to trophic position 3. Most studies were performed in a multitude of habitats (32) and 14 in forest, while 74 % of the studies were made in tropical areas and 26 % in temperate areas.

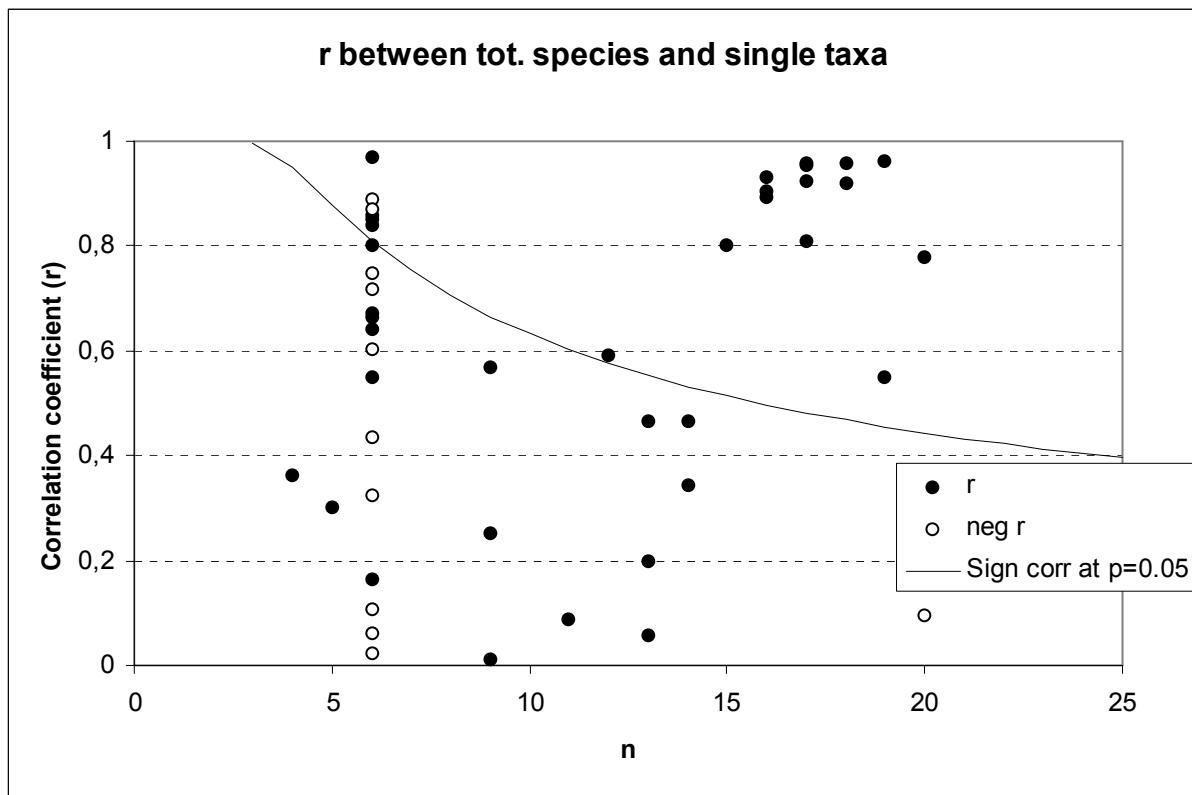


Figure 4. The distribution of correlation coefficients (r) and sample sizes (n) in the data set with the comparison of total number of species and single taxa in a group. The line indicates the values of r that are significant at $p = 0.05$, the points above the line being significant. Open dots indicate negative correlations.

META-ANALYSIS

All correlations in the data set

The overall average correlation coefficient r between the richness of two taxa in the data set was 0.373 (95 % confidence limits ± 0.059 ; back transformed from z-transformed correlations for random model), which significantly differed from 0 (fig 5). The total variance in species richness of one group explained by species richness in another group was therefore on average 14 % ($0.373^2 * 100$). The values of the correlations varied greatly though (fig 3), indicated by the fact that the homogeneity statistic Q was highly significant ($Q = 1731$; $p << 0.05$, $df = 502$) (fig 5). This shows that the random effects model is the appropriate one to use, and that there is no underlying single general effect size (correlation) that has been estimated.

Subdivisions of data

There was no significant difference within the subsets of area classes (fig 5). However, the difference between correlations of area class 1 and 2 was very close to significant ($r = 0.243$, 95 % CL 0.159-0.327 vs. $r = 0.504$, 95 % CL 0.326-0.682, respectively).

When comparing the average correlation in the different taxonomic distance classes I found that the average correlation of between genera - within families (class 1) was higher than in all other comparisons (classes 2-4) except between kingdoms (class 5). The average correlation in taxonomic distance class 5 was higher than in class 2 (fig 5). There was significant heterogeneity in all taxonomic classes, which indicates that taxonomic distance was not a major factor explaining the variation in the richness correlations examined.

The average correlation between taxa in trophic position 1 (autotrophs vs. autotrophs) was significantly lower than the ones for trophic position 2 (autotrophs vs. heterotrophs) and 3 (heterotrophs vs. heterotrophs) (fig 5).

The average correlations did not differ between the different climatic belts (fig 5).

Among the different biotopes, the forest category had a significantly higher average correlation than both categories multi and semi-natural pasture (fig 5), while desert had a very high CL (0.679 ± 1.215 , $n = 2$) and did not differ from the other categories or even from 0.

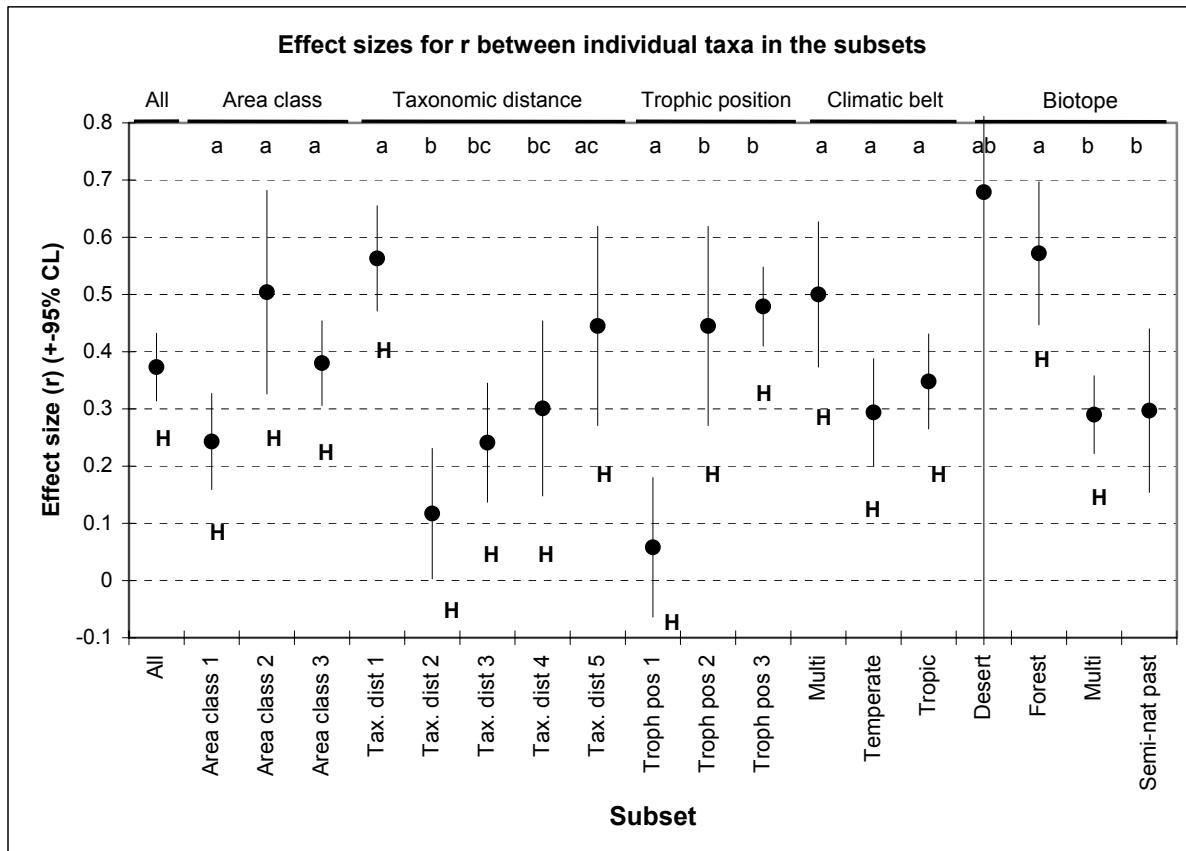


Figure 5. Effect sizes for richness correlations between individual taxa. Area class 1 includes the smallest areas, and class 3 the largest areas. Taxonomic distance increases with increasing class number. Trophic position 1 includes correlations between autotrophs, 2 between autotrophs and heterotrophs and 3 between heterotrophs. Within subsets categories with the same letters "a, b, c" do not differ significantly from each other. H indicates that the correlation coefficients in the category are heterogeneous.

One of the references, Roos et al. (2004), provided 190 correlation coefficients between plant families. The r-values varied greatly and ranged from -0.975 to 0.995 , and the average effect size was merely $0.058 (\pm 0.122)$. This value probably lowered the overall average effect size, and could contribute to a biased estimate of the correlation between groups in other comparisons – at least the study may have been given too high a weight in the overall analysis. Therefore I removed these data to see if and how the results changed. The overall average effect size increased from 0.373 to 0.478 (fig 6). Since all of the 190 correlations in this study were allocated to area class 3, removing them increased the average effect size for this class from 0.38 to 0.559 , which became significantly different from the average effect size of area class 1. The average effect size for taxonomic distance class 2 increased from 0.117 to 0.453 . The average effect size for the tropics increased from 0.348 to 0.575 and by this it became

significantly different from the average effect size of the temperate areas. Furthermore, the correlation coefficients from Roos et al. (2004) were the only ones in trophic position 1, so this class is absent from figure 6.

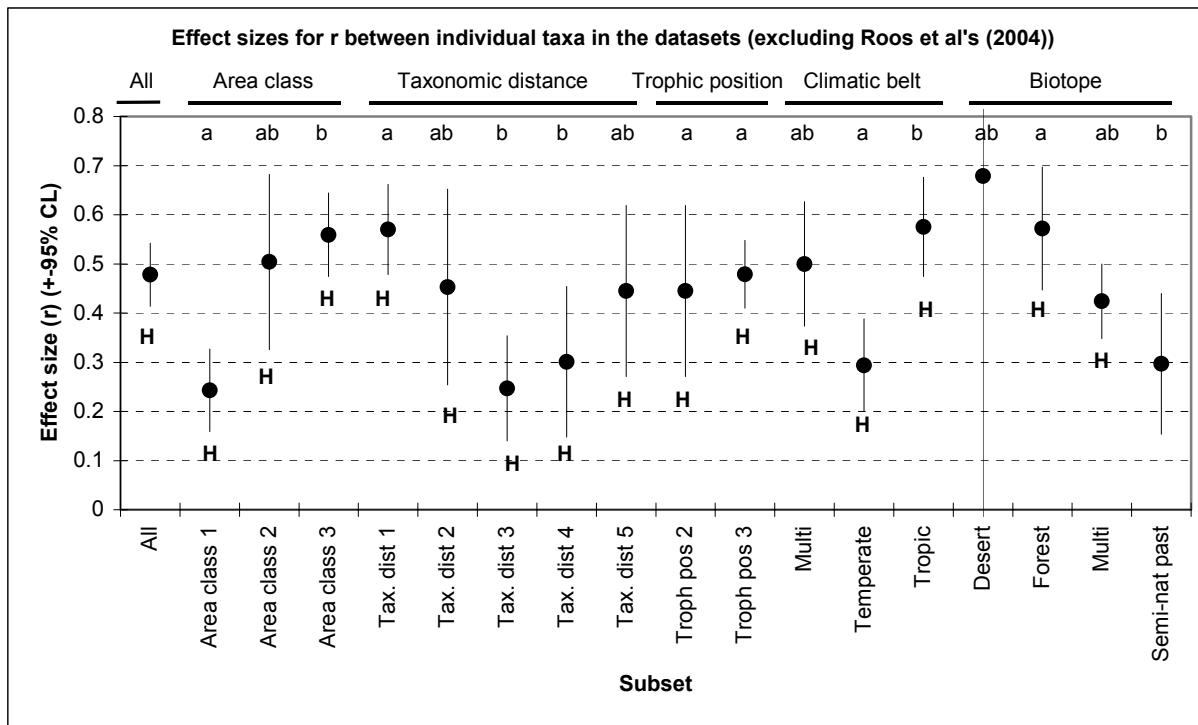


Figure 6. Effect sizes for richness correlations between individual taxa, excluding Roos et al (2004), which contained all plant-plant correlations (i.e. trophic position 1, that therefore is not included). Notation as in figure 5.

Correlations between total number of species and individual taxa in a group

The overall average correlation coefficient (r) was $0.580 (\pm 0.248)$ when comparing total number of species and individual taxa from the three references providing such data. There was no significant difference between the average correlations of the different subsets of data (fig 7). However, the overall average r significantly differed from 0 and the total variance in total species richness explained by species richness in one taxon was $33.6\% (0.580^2 * 100)$.

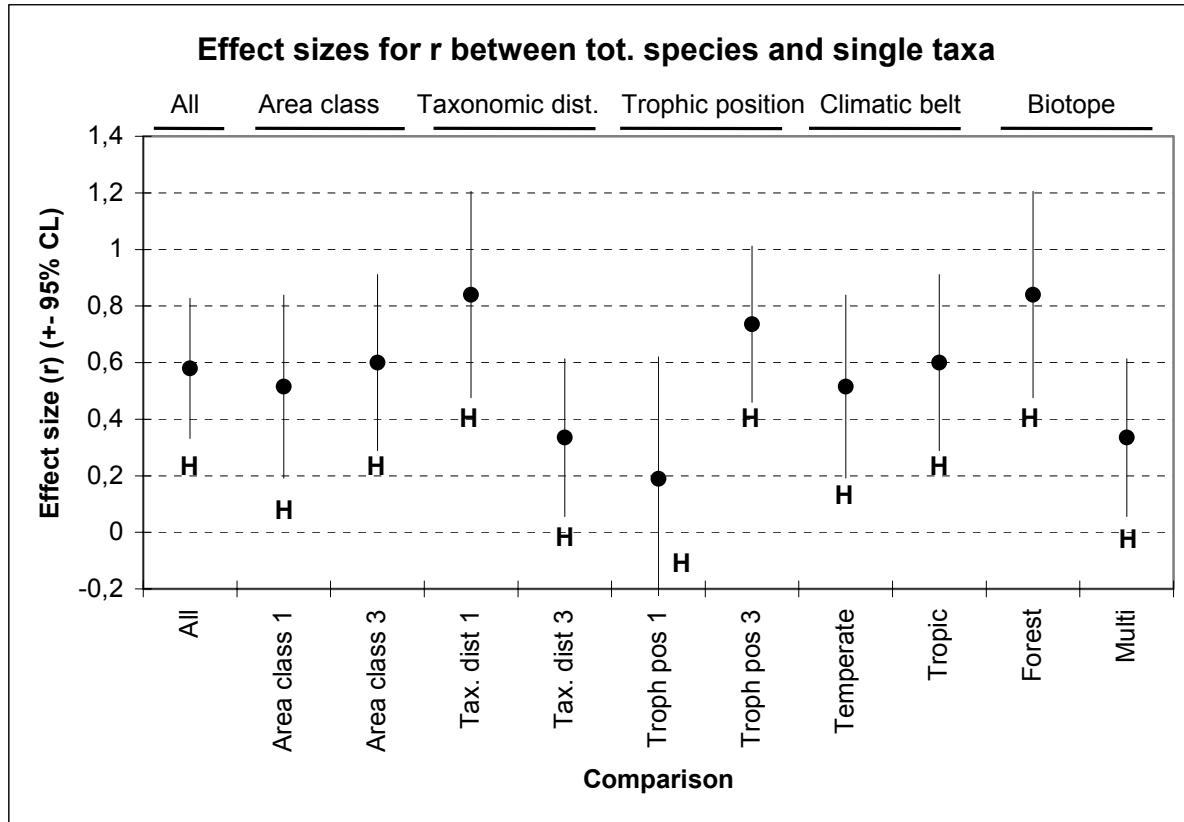


Figure 7. Effect sizes for richness correlations between individual taxa and all species in a group. Area class 1 include the smallest areas, and class 3 the largest areas. Taxonomic distance increase with increasing class number. Trophic position 1 includes correlations between autotrophs, and 3 between heterotrophs. H indicates that the correlation coefficients in the category are heterogeneous.

DISCUSSION

In my study I found that the average correlation coefficient r between species richness of different taxa was $0.373 (\pm 0.059)$, which is significantly different from 0. However, the heterogeneity was high among the different studies. One of the examined factors that could explain some of the heterogeneity in the total data set was the taxonomic distance between the correlated groups. The average correlation in different taxonomy classes differed significantly in several pairwise comparisons. The highest correlations were found in studies examining richness correlations in the lowest level (in this study), taxonomic distance class 1 (different families within the same order).

Wolters et al. (2006) made a study similar to mine and found an average correlation r of $0.374 (\pm 0.068)$, which is practically the same result as I found ($0.373 (\pm 0.059)$).

I found that only 31 % of all correlations were significant, and of all correlations 4 % were significantly negative. This indicates that species richness of different taxa often is not spatially covariant. However, my study includes diverse kinds of pairs of taxa that are not always expected to be interacting, and hence might be regarded not to be appropriate for correlation studies aimed at identifying e.g. indicator taxa.

Methodological aspects

By using meta-analysis methods I examined if estimates of species richness of different taxa in general or under certain *a priori* defined circumstances were correlated. The problem that sampling effort and hence precision of the estimates of the correlation coefficients varied between studies, could be partly overcome by weighting the studies according to their sample sizes. My results show that studies with groups in taxonomic distance class 1 and/or in the forest biotope seem to have the highest predictive power (fig 5). However, none of the taxa were found to be a particularly good universal indicator for all classes the dataset was divided into.

The method to correlate residuals, which I have used in my study, is a debated method in other areas of ecology (e.g. Schulte-Hostedde et al., 2004). However, in the present case it was the only one judged possible to account for the species-area relation. Since the species-area relation usually becomes linear with the log-transformation this form was regarded most appropriate, despite the fact that untransformed richness values usually are used (e.g. Wolters et al., 2006). However, the differences are likely to be negligible.

Though as many as 503 correlations are included in my analysis, there were only 20 independent studies, and the selection of taxa is uneven. Only one study provided correlations for plant-plant relationships (trophic position 1), which makes the results on this question uncertain. The test of the hypothesis that there is a higher correlation between plants and animals than between plants and plants or animals and animals, thus becomes doubtful.

Just as the number of species most often increases with area, it also increases with time spent searching for species (sampling effort). The former I have compensated for but not the latter. I made the assumption that researchers performing the studies have considered the species-time relationship and made adequate samplings (or appropriate compensations). When the species-area relationship is significant there is often a large difference between correlations calculated from area-compensated data (residuals) and data not area-compensated. If the species-area relationship is insignificant the difference is not as apparent. To illustrate these differences I made a comparison between correlations from area-compensated data and data not area compensated (table 2). Data from Nilsson et al. (1988) (and Ahlén et al. 1982 and Bengtsson et al., unpublished) and Krasnov et al. (2004) have highly significant species-area relationships, while this relationship is insignificant in Williams' (1982) data and Söderström et al.'s (2001) data (for all taxa except for dung beetles, which showed a negative relation with area). For data with significant species-area relationships it seems that correlations from data not compensated for area are frequently higher than the ones from area compensated data, and they are never negative. To conclude, when the relationship between area and species number is significant it should be taken into account when calculating correlations between taxa or representative results will not be obtained, as is apparent in table 2. However, for sake of consistency, I treated the data equally and calculated the residuals regardless of the status of the species-area relationship.

Table 2. Comparison between area compensated data calculated according to the procedure described in Materials and methods, and data not area compensated where r's (correlations) are calculated from log species number. Correlations with an asterisk (*) are significant at the 5 % level.

| Reference | Taxon | Taxon | Area comp. r's | Not area comp. r's |
|---|---------------|-----------------|-------------------|-----------------------|
| Nilsson et al., 1988 | Carabids | Land snails | 0.548904* | 0.74188* |
| Nilsson et al., 1988 | Carabids | Woody plants | 0.259858 | 0.680113* |
| Nilsson et al., 1988 and Bengtsson et al., unpubl. & Holt et al. 1999 | Carabids | Spiders | 0.249538 | 0.655487* |
| Nilsson et al., 1988 and Ahlén et al., 1982 | Carabids | Birds | -0.18302 | 0.635162* |
| Nilsson et al., 1988 | Land snails | Woody plants | 0.389988 | 0.661652* |
| Nilsson et al., 1988 and Bengtsson et al., unpubl. & Holt et al. 1999 | Land snails | Spiders | 0.197321 | 0.546805* |
| Nilsson et al., 1988 and Ahlén et al., 1982 | Land snails | Birds | -0.23778 | 0.479007 |
| Nilsson et al., 1988 and Bengtsson et al., unpubl. & Holt et al. 1999 | Woody plants | Spiders | -0.56785* | 0.300727 |
| Nilsson et al., 1988 and Ahlén et al., 1982 | Woody plants | Birds | -0.45003 | 0.583537* |
| Nilsson et al., 1988 Bengtsson et al., unpubl. & Holt et al., 1999, and Ahlén et al., 1982 | Spiders | Birds | 0.203733 | 0.721979* |
| Krasnov et al., 2004 | Small mammals | Fleas | 0.596514* | 0.765528* |
| Williams, 1982 | Lepidoptera | Diptera | 0.752109 | 0.850851* |
| Williams, 1982 | Lepidoptera | Coleoptera | 0.924966* | 0.954771* |
| Williams, 1982 | Lepidoptera | Vascular plants | 0.906112* | 0.80875 |
| Williams, 1982 | Diptera | Coleoptera | 0.860718* | 0.919267* |
| Williams, 1982 | Diptera | Vascular plants | 0.564412 | 0.579152 |
| Williams, 1982 | Coleoptera | Vascular plants | 0.70584 | 0.714182 |
| Söderström et al., 2001 | Butterflies | Bumblebees | 0,527036* | 0,526673* |
| Söderström et al., 2001 | Butterflies | Dung beetles | 0,617264* | 0,456984* |
| Söderström et al., 2001 | Butterflies | Birds | 0,275511 | 0,252655 |
| Söderström et al., 2001 | Butterflies | Plants | 0,369913 | 0,361878 |
| Söderström et al., 2001 | Bumblebees | Dung beetles | 0,189682 | 0,164259 |
| Söderström et al., 2001 | Bumblebees | Birds | 0,152806 | 0,136966 |
| Söderström et al., 2001 | Bumblebees | Plants | 0,20981 | 0,19871 |
| Söderström et al., 2001 | Dung beetles | Birds | -0,05431 | -0,18978 |
| Söderström et al., 2001 | Dung beetles | Plants | 0,219777 | 0,102317 |
| Söderström et al., 2001 | Birds | Plants | 0,508718* | 0,530573* |

The difference between the previously mentioned study of Wolters et al. (2006) and my study is that Wolters et al. (2006) examined published correlation coefficients while I calculated correlation coefficients from published species-area relationships. Wolters et al. (2006) found unexpectedly few negative correlations (only 5 of 152) and they discussed whether this was due to a publication bias against negative correlations or if it was real. Since I have not, unlike Wolters et al. (2006), examined published correlations, my results should not be biased against negative correlations. In my study 146 of 503 correlations were negative. According to a G-test there was a highly significant difference ($G = 57.01$, $p < 0.05$) between the proportion of negative correlations in Wolters et al. (2006) and in this study.

Hypotheses

The hypothesis (1) that more closely related taxa are more correlated than taxa further apart taxonomically receives support in my results. Correlations between families in the same order (taxonomic distance 1) were significantly higher than correlations in all other taxonomic classes except the one between kingdoms (tax. dist. 5), i.e., correlations between plants and animals. This latter correlation is the same as the one for trophic position 2, which according to my hypothesis (2) should be high. In the subset with trophic positions, the average correlation in class 2 (plants-animals) is higher than in class 1 (plants-plants) but not significantly different from the average in class 3 (animals-animals), thus these results disagree with my hypothesis (2). Perhaps the correlations in class 3 are high due to interactions among some of the animal groups that thus had high correlations. If I had had the time, I would have found it interesting to select pairs of taxa known to interact (like plants-herbivores/pollinators, parasites-hosts etc.) and compared them to pairs of taxa unlikely to interact. It would also have been interesting to see whether correlations within families – between genera (tax. dist. 0) are even higher than the ones in taxonomic class 1, however there were no correlations allocated to this class in this study.

Furthermore, there were only a few habitats studied. Most studies (77 %) were performed in a multitude of habitats, which makes it difficult to make any predictions about correlations from certain habitats having possibly higher prediction power than others. The forest biotope had a significantly higher average correlation than both multiple habitats and seminatural pasture so perhaps it has a higher prediction power than other habitats. However, this conclusion may not be valid since so few habitats were included and because of the uneven distribution of correlations in the compared habitats.

As mentioned in the introduction predictions about correlation magnitude at different spatial scales are very difficult to make and my results showed no significant differences between the correlations in the three area classes. A question is how relevant it is to investigate the correlation between groups on very large spatial scales (entire countries for example) since any information gained is difficult to apply in practice, for example when establishing a nature reserve.

Further investigating the hypothesis concerning taxonomic distance (1)

To further investigate the correlations on different taxonomic levels, I chose the two studies most numerous in correlations and calculated the Spearman-rank correlation coefficient (r_s) between r and taxonomic distance for each study. The data on plant families from Roos et al. (2004) were according to my system of taxonomic classes (fig 1) divided into classes 1, 2 and 3, however according to the tree of life web project (www.tolweb.org) the classification was not so obvious. Some groups seemed to be more closely related than others even though they had to be allocated to the same taxonomic class according to my system. To distinguish in more detail

between the taxonomic levels I divided the correlations into 6 new taxonomic classes (0-5) where class 0 included taxa most closely related and class 5 taxa most distantly related. My hypothesis was that correlations in class 0 would be highest and the ones in class 5 lowest. For data from Roos et al. (2004) the Spearman-rank correlation coefficient was not significant and hence there were no differences between the classes. The data on butterfly families and subfamilies from Beccaloni and Gaston (1994) were originally allocated to taxonomic distance class 1, but with a more detailed system I could separate the correlations into 3 classes (1-3), where class 1 included taxa most closely related and class 3 taxa most distantly related. The Spearman rank correlation coefficient showed a tendency for the correlation to increase with increasing taxonomic distance, however it was not significant. To conclude, I found no support for this hypothesis in these subsets of the data.

Correlations between the same groups differ among sites

In table 3 all correlations between plants and birds are listed. Plants and birds can be expected to be correlated since a high diversity of plants should provide a high diversity of food resources (either the plants themselves or insect diversity dependant of the plants) and/or habitat diversity for birds, which would lead to high bird diversity. Seven of the 11 correlations are significant and 4 are non-significant. One of the lowest correlations is between sea birds and plants and its insignificance might be due to that these groups are not interacting strongly (as are land birds and plants for example). Two of the insignificant correlations are both from Sweden and are the only ones in the forest biotope. However, that this should be the explanation to the low correlations seems unlikely, since forest had a high average correlation when comparing the subsets in the whole dataset (fig 5). To sum up, the results shown in table 3 indicates a general positive correlation between the diversity of plants and birds and with further research perhaps it can be explored if these groups are possible indicator taxa of the diversity of each other.

Table 3. Correlations between plants and birds. All correlations are allocated to taxonomic distance class 5, and trophic position 3. Correlations marked with an asterisk (*) are significant at the 5 %-level, n = number of plots, r = correlation coefficient.

| Reference | Taxa | Taxa | n | r | Region | Area class | Biotope | Clim. belt |
|---|------------|--------------|----|-----------|----------------------------|------------|----------------------|------------|
| Amerson, 1975 | Birds | Plants | 10 | 0.754597* | N-W Hawaiian islands | 1 | low sandy islands | Tropic |
| Bisconti et al., 2001 | Birds | Plants | 10 | 0.487445 | Galapagos islands | 2 | multi | Tropic |
| Chown et al., 1998 | Land birds | Plants | 24 | 0.621965* | Southern ocean islands | 2 | multi | Temp. |
| Chown et al., 1998 | Sea birds | Plants | 24 | 0.079939 | Southern ocean islands | 2 | multi | Temp. |
| Connor et al., 1978 | Birds | Plants | 15 | 0.518126* | Galapagos islands | 2 | multi | Tropic |
| Hansson, 1997 | Birds | Plants | 27 | 0.038379 | Sweden | 1 | forest | Temp. |
| Kitchener et al., 1980 a and Kitchener et al., 1982 | Birds | Plants | 22 | 0.430715* | Australia (wheatbelt) | 1 | multi | Tropic |
| Lack, 1969 | Birds | Plants | 7 | 0.953838* | Canary islands | 2 | multi | Tropic |
| Nilsson et al., 1988 and Ahlén et al., 1982 | Birds | Woody plants | 17 | -0.45003 | Sweden | 1 | forest | Temp. |
| Söderström et al., 2001 | Birds | Plants | 31 | 0.508718* | Sweden | 1 | semi-natural pasture | Temp. |
| Wright, 1981 and Moody, 2000 | Birds | Plants | 8 | 0.83624* | California channel islands | 2 | multi | Temp. |

Indicators

For a species group to be a good indicator its species richness should be similar to the species richness of the group you wish to predict. Preferably large groups (or perhaps several groups combined) should be used as indicators, since the larger the group the proportionally less every species contribute to the group total and thus the less each species will influence the prediction of species richness (Beccaloni and Gaston, 1994).

Are there some groups that appear to be more useful as indicators than others? In this dataset, four pairs of taxa had been studied by different authors (table 4). Of these groups, plants seem to be quite well correlated with insects and also often with birds. Hence, perhaps plants is a good general indicator taxon for predicting species richness of some animal groups, especially since animals frequently are dependent of plants as habitats or food resources (primarily or secondarily by eating organisms that use plants as a food resource).

Table 4: Mean correlation between four pairs of taxa that had been studied by several authors.

| Taxa | Taxa | Mean $r \pm 95\%CL$ | References |
|-------------|-------------|---------------------------------------|---|
| Birds | Plants | 0.464 ± 0.299 | Amerson, 1975, Bisconti et al., 2001, Chown et al., 1998, Connor et al., 1978, Hansson, 1997, Kitchener et al., 1980 a and Kitchener et al., 1982, Lack, 1969, Nilsson et al., 1988 and Ahlén et al., 1982, Söderström et al., 2001, Wright, 1981 and Moody, 2000 |
| Birds | Bats | 0.715 ± 0.793 | Davila et al., 2002, Kattan et al., 2004, Ricklefs et al., 1999 |
| Birds | Insects | 0.371 ± 0.298 | Chown et al., 1998, Kattan et al., 2004, Lack, 1969, Nilsson et al., 1988 and Ahlén et al., 1982, Ricklefs et al., 1999, Söderström et al., 2001 |
| Plants | Insects | 0.559 ± 0.331 | Chown et al., 1998, Lack, 1969, Nilsson et al., 1988, Söderström et al., 2001, Williams, 1982 |

Besides richness correlations between taxa there are other indicators for biodiversity. Potential indicators, apart from diversity of well-known taxa, are species of conservation concern and landscape features or vegetation types. If the distributions of the members of an indicator group are representative of a larger set of organisms, sites selected to include these members have the potential to cover a large proportion of organisms outside the group. Rare species are often those most likely to be lost if not protected and it is therefore crucial to understand at what degree they are included in sites selected for conservation if indicator groups are to be used as tools (Lawler et al., 2002).

Care must be taken when suggesting that one organism group can be used as a general biodiversity indicator. On the other hand, if we want to preserve species, reserves needs to be established and if total inventories is not an option some kind of diversity indicator has to be used. A good universal indicator might be difficult to find, but more thorough inventories for correlation calculations at appropriate spatial scales could perhaps make it possible to discover regional or local indicator groups. Different conditions might apply in different biotopes for instance. To discover the true connections and possible causes of correlation between diversity of different taxa, more research is needed in this field.

CONCLUSION

In my study I found the average correlation between taxa to be 0.373 (95 % CL = 0.059). This indicates positive but weak correlations between taxa in the very heterogeneous dataset. The total variance in species richness of one group explained by species richness in another group was on average 14 %.

It is obvious that the species richness of plants and animals are positively correlated at the global scale, since both groups increase into the tropics (Hawkins et al. 2003). These connections could be real also at a smaller regional or local scale, they just need to be examined more closely. This might be possible with studies performed at suitable spatial scales and including many taxa sampled with equivalent methods.

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Appendices

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APPENDIX 1

Number of correlations per taxa

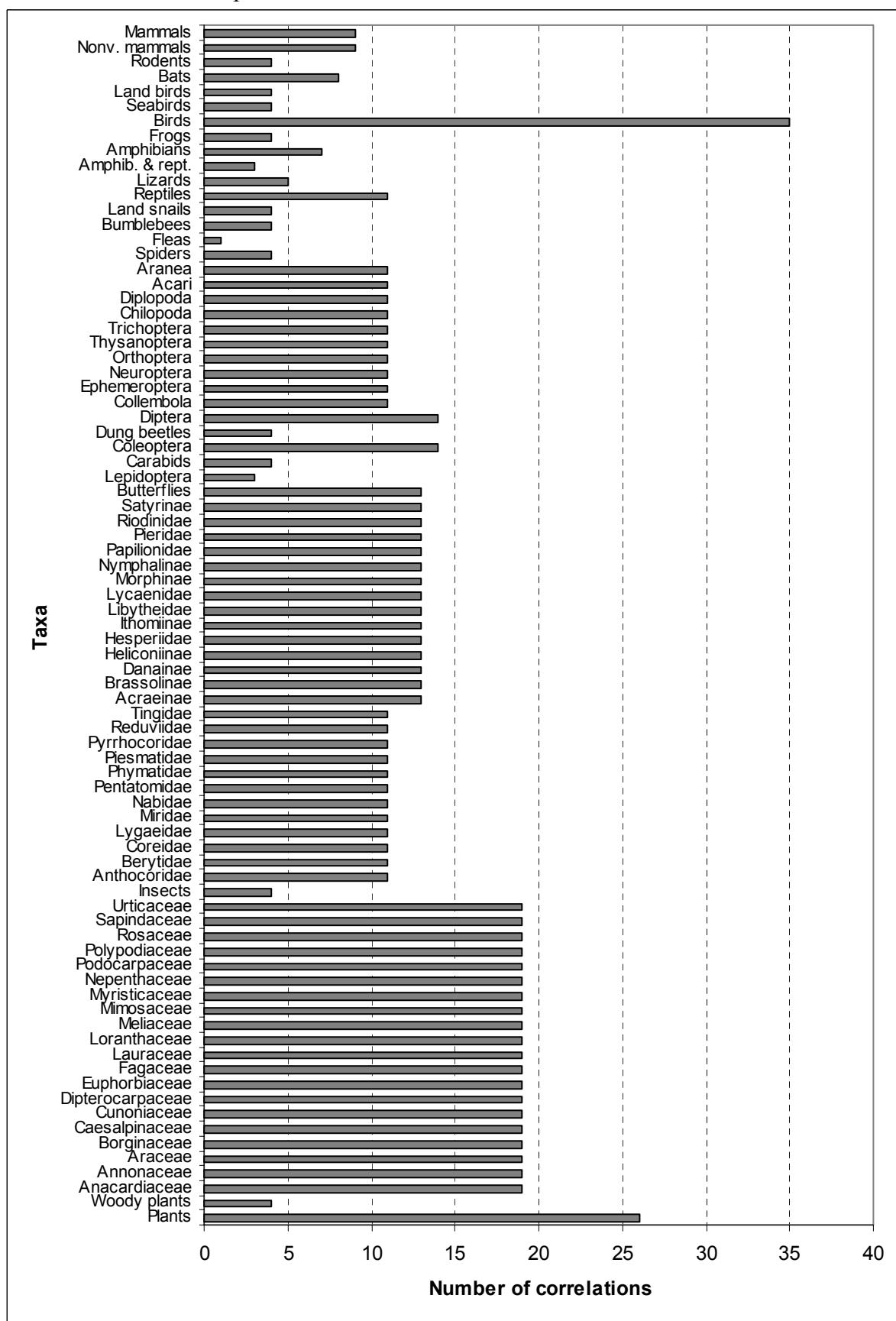
APPENDIX 2

Distribution of positive significant, negative significant and non-significant correlations in the entire dataset and in the different subsets.

APPENDIX 3.

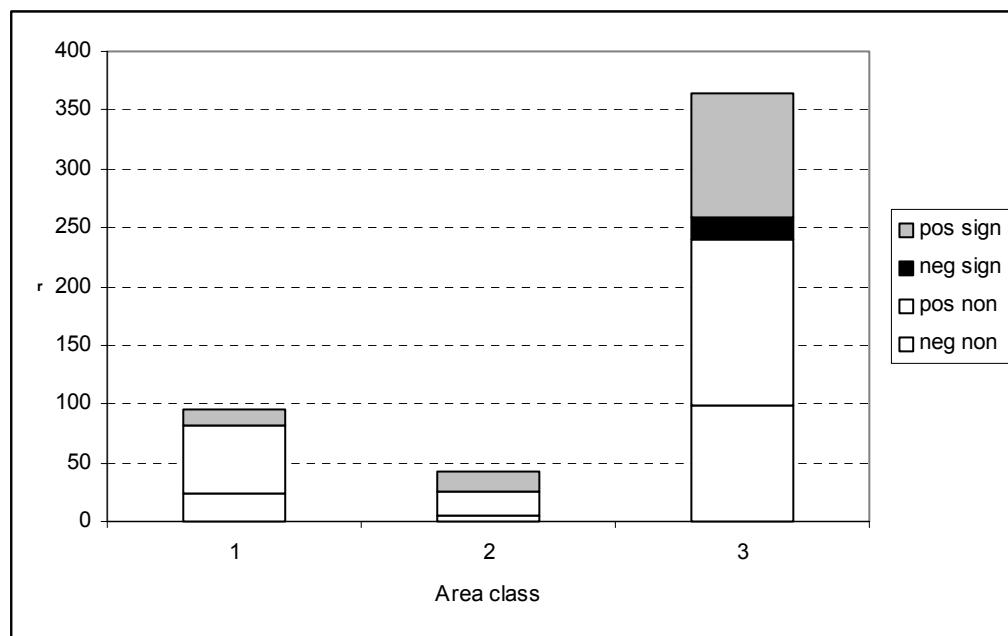
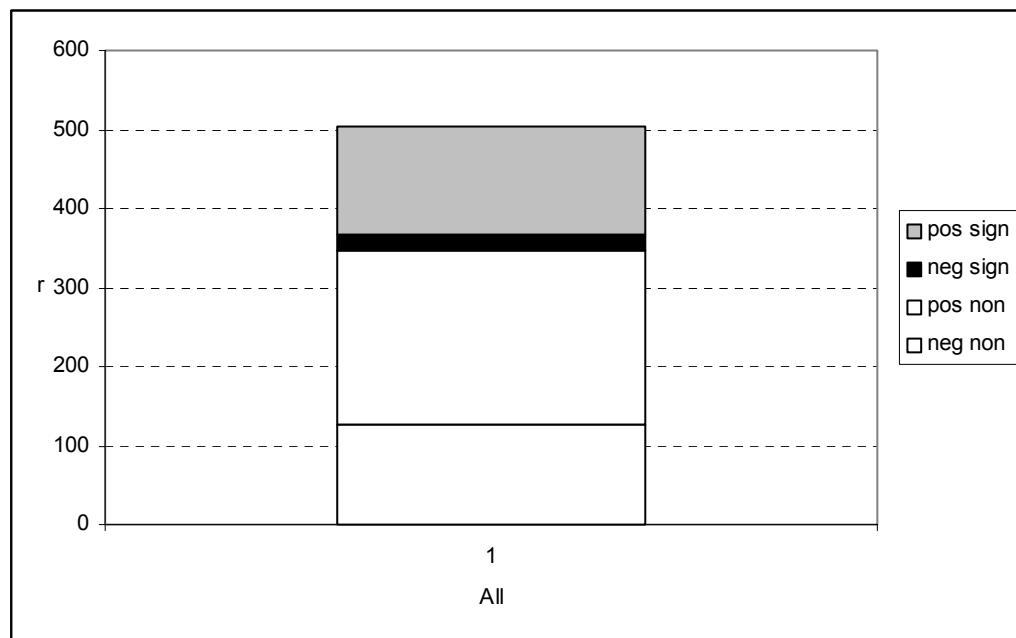
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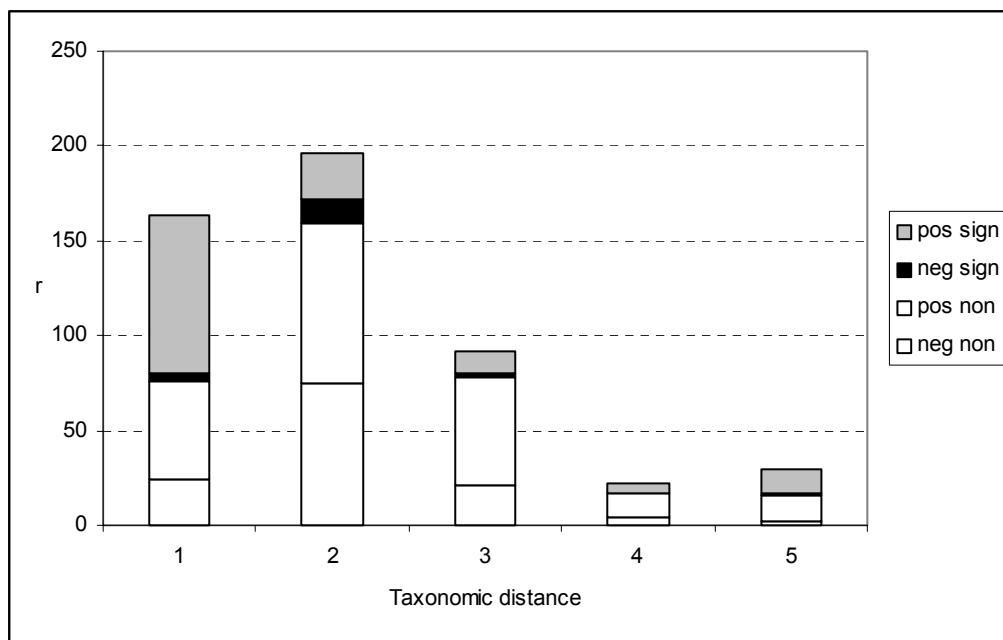
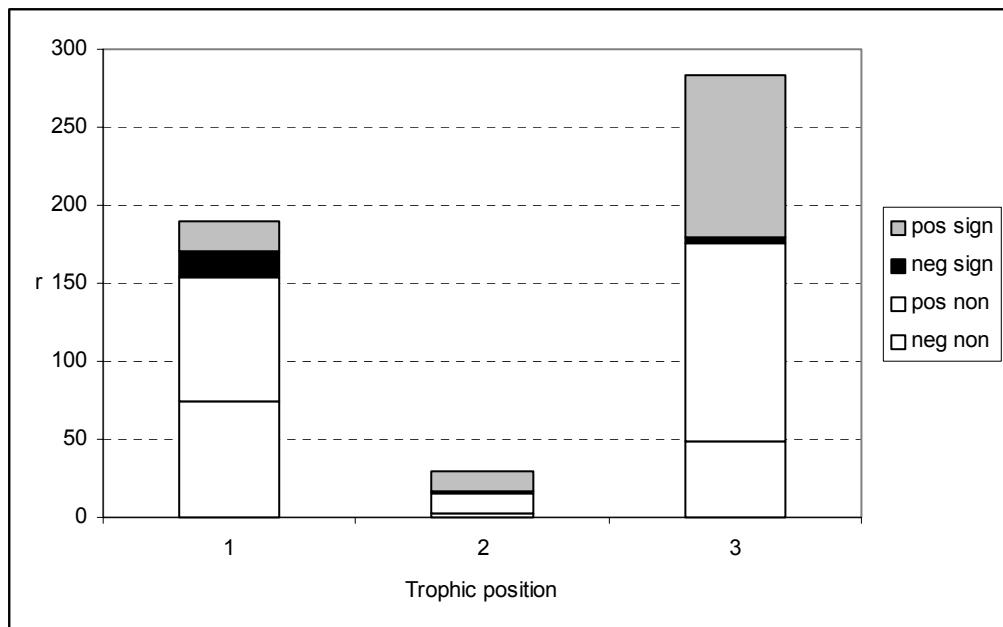
APPENDIX 1
Number of correlations per taxa

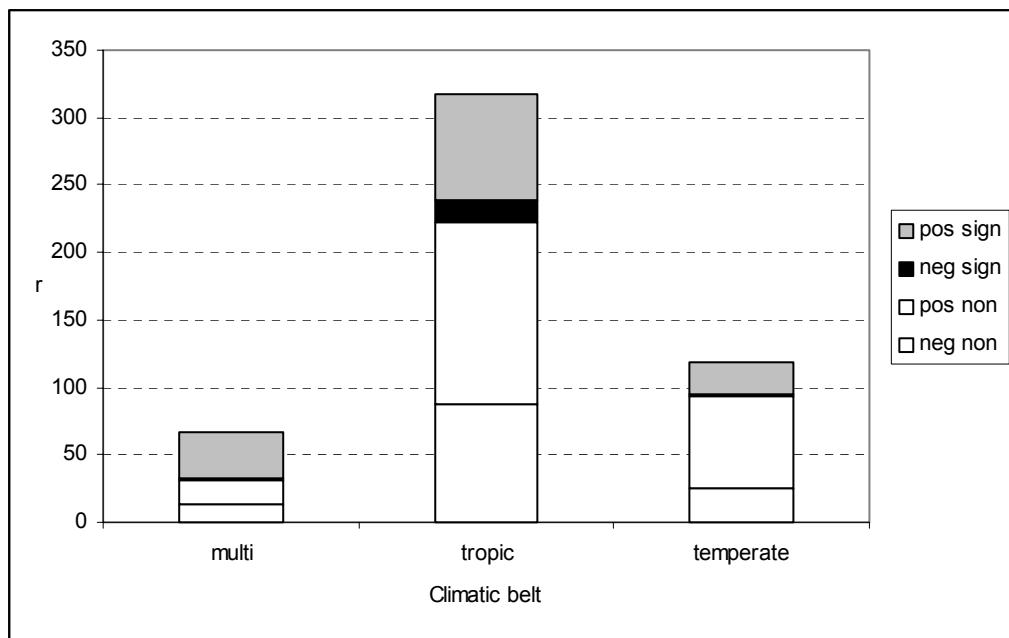
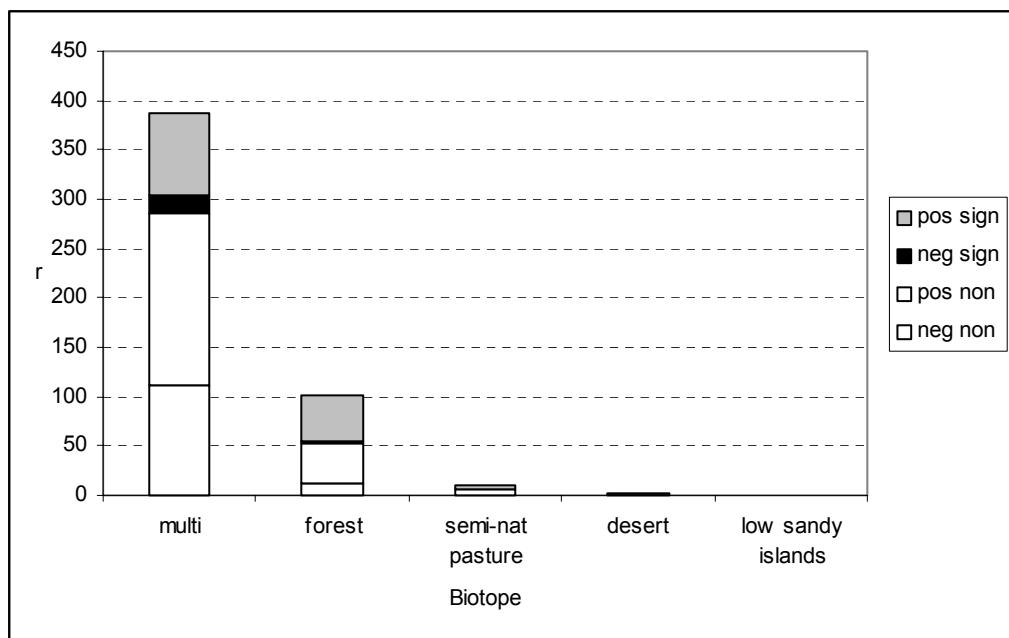


APPENDIX 2

Distribution of positive significant, negative significant and non-significant correlations in the entire dataset and in the different subsets.







APPENDIX 3. Collection of data.

| Reference | Taxon | r | n | Area class | Tax. dist. | Troph. position | Biotope | Clim. belt | Location |
|---------------|---------------|--------|----|------------|------------|-----------------|-------------------|------------|----------------------|
| Amerson, 1975 | Birds | 0,755 | 10 | 1 | 5 | 2 | low sandy islands | tropic | N-W Hawaiian Islands |
| Baldi, 2003 | Collembola | 0,102 | 11 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Collembola | 0,404 | 9 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Collembola | 0,421 | 9 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Collembola | 0,356 | 4 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Trichoptera | 0,400 | 9 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Thysanoptera | 0,705 | 5 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Coleoptera | 0,026 | 11 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Aranea | 0,263 | 11 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Diplopoda | -0,398 | 11 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Chilopoda | -0,262 | 11 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Diptera | -0,076 | 11 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Neuroptera | 0,059 | 9 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Orthoptera | 0,378 | 9 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Ephemeroptera | 0,325 | 4 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Trichoptera | 0,782 | 9 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Thysanoptera | 0,586 | 5 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Coleoptera | -0,132 | 13 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Aranea | 0,510 | 12 | 1 | 2 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Diplopoda | -0,301 | 13 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Chilopoda | -0,300 | 13 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Diptera | 0,161 | 13 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Orthoptera | 0,368 | 9 | 1 | 2 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Ephemeroptera | -0,910 | 4 | 1 | 2 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Trichoptera | -0,307 | 9 | 1 | 2 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Thysanoptera | 0,329 | 5 | 1 | 2 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Coleoptera | 0,472 | 9 | 1 | 2 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Aranea | 0,618 | 9 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Diplopoda | 0,462 | 9 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Chilopoda | 0,382 | 9 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Diptera | 0,519 | 9 | 1 | 2 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Orthoptera | 0,375 | 4 | 1 | 2 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Ephemeroptera | 0,232 | 9 | 1 | 2 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Trichoptera | 0,344 | 5 | 1 | 2 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Thysanoptera | 0,344 | 5 | 1 | 2 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Coleoptera | -0,002 | 9 | 1 | 2 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Aranea | 0,140 | 9 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Diplopoda | -0,174 | 9 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Chilopoda | -0,173 | 9 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Diptera | 0,414 | 9 | 1 | 2 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Orthoptera | 0,516 | 4 | 1 | 2 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Ephemeroptera | 0,993 | 4 | 1 | 2 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Trichoptera | 0,310 | 4 | 1 | 2 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Thysanoptera | -0,443 | 4 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Coleoptera | -0,650 | 4 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Diplopoda | -0,821 | 4 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Chilopoda | 0,327 | 4 | 1 | 2 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Diptera | 0,729 | 5 | 1 | 2 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Orthoptera | 0,002 | 9 | 1 | 2 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Ephemeroptera | 0,359 | 9 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Trichoptera | -0,268 | 9 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Thysanoptera | -0,319 | 9 | 1 | 3 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Coleoptera | -0,163 | 9 | 1 | 2 | 3 | multi | temperate | Hungary |
| Baldi, 2003 | Diplopoda | 0,317 | 5 | 1 | 2 | 3 | multi | temperate | Hungary |

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|---|--------|----|-------|---------------------------|
| Becker, 1992 | 3 | 3 | multi | World |
| Becker, 1992 | 3 | 3 | multi | World |
| Becker, 1992 | 3 | 3 | multi | World |
| Bisconti et al., 2001 | -0,141 | 21 | 3 | World |
| Bisconti et al., 2001 | 0,504 | 21 | 3 | Galapagos islands |
| Case, 1975 | 0,425 | 22 | 3 | Galapagos islands |
| Chown et al., 1998 | -0,043 | 15 | 2 | Galapagos islands |
| Chown et al., 1998 | 0,487 | 10 | 2 | Galapagos islands |
| Chown et al., 1998 | -0,073 | 10 | 2 | Gulf of California |
| Chown et al., 1998 | 0,344 | 24 | 2 | Southern ocean islands |
| Chown et al., 1998 | 0,798 | 24 | 2 | Southern ocean islands |
| Chown et al., 1998 | 0,080 | 24 | 2 | Southern ocean islands |
| Chown et al., 1998 | 0,622 | 24 | 2 | Southern ocean islands |
| Chown et al., 1998 | 0,189 | 16 | 2 | Southern ocean islands |
| Chown et al., 1998 | 0,222 | 25 | 2 | Southern ocean islands |
| Chown et al., 1998 | 0,777 | 24 | 2 | Southern ocean islands |
| Chown et al., 1998 | 0,100 | 16 | 2 | Southern ocean islands |
| Chown et al., 1998 | -0,009 | 24 | 2 | Southern ocean islands |
| Chown et al., 1998 | 0,222 | 25 | 2 | Southern ocean islands |
| Chown et al., 1998 | -0,738 | 16 | 2 | Southern ocean islands |
| Chown et al., 1998 | 0,246 | 16 | 2 | Southern ocean islands |
| Chown et al., 1998 | 0,518 | 15 | 2 | Southern ocean islands |
| Davila et al., 2002 | 0,928 | 5 | 3 | USA |
| Hansson, 1997 | 0,038 | 27 | 1 | Sweden |
| Kattan et al., 2004 | 0,374 | 10 | 3 | Colombia |
| Kattan et al., 2004 | 0,533 | 11 | 3 | Colombia |
| Kattan et al., 2004 | 0,044 | 11 | 3 | Colombia |
| Kattan et al., 2004 | 0,245 | 11 | 3 | Colombia |
| Kattan et al., 2004 | 0,270 | 10 | 3 | Colombia |
| Kattan et al., 2004 | 0,021 | 10 | 3 | Colombia |
| Kattan et al., 2004 | 0,052 | 10 | 3 | Colombia |
| Kattan et al., 2004 | 0,357 | 11 | 3 | Colombia |
| Kattan et al., 2004 | 0,829 | 11 | 3 | Colombia |
| Kattan et al., 2004 | 0,684 | 11 | 3 | Colombia |
| Kattan et al., 2004 | 0,569 | 23 | 1 | Australia (wheatbelt) |
| Kitchener et al., 1980 a | 0,277 | 23 | 1 | Australia (wheatbelt) |
| Kitchener et al., 1980 a and | 0,431 | 22 | 1 | Australia (wheatbelt) |
| Kitchener et al., 1980 b | 0,398 | 23 | 1 | Australia (wheatbelt) |
| Kitchener et al., 1980 a and | 0,661 | 22 | 1 | Australia (wheatbelt) |
| Kitchener et al., 1980 b | 0,219 | 22 | 1 | Australia (wheatbelt) |
| Kitchener et al., 1980 a and | 0,140 | 12 | 1 | Australia (ocean islands) |
| Kitchener et al., 1980 b | 0,597 | 37 | 3 | World |
| Krasnov et al., 2004 | 0,954 | 7 | 2 | Canary islands |
| Lack, 1969 | 0,902 | 7 | 2 | Canary islands |
| Lack, 1969 | 0,936 | 7 | 2 | Canary islands |
| Niisson et al., 1988 | 0,549 | 17 | 1 | Sweden |
| Niisson et al., 1988 | 0,260 | 17 | 1 | Sweden |
| Niisson et al., 1988 and Bengtsson et al., unpubl. & Holt et al. 1999 | 0,250 | 17 | 1 | temperate |
| Niisson et al., 1988 and Ahlén et al., 1982 | -0,183 | 17 | 1 | Sweden |
| Niisson et al., 1988 | 0,390 | 17 | 1 | temperate |
| | | | 3 | temperate |
| | | | 2 | temperate |

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|--------------|---------------|-------|---|---|---|--------|
| Becker, 1992 | Piesmatidae | multi | 1 | 3 | 3 | 14 |
| Becker, 1992 | Berytidae | multi | 1 | 3 | 3 | 0,222 |
| Becker, 1992 | Pyrrhocoridae | multi | 1 | 3 | 3 | 0,421 |
| Becker, 1992 | Coreidae | multi | 1 | 3 | 3 | -0,488 |
| Becker, 1992 | Nabidae | multi | 1 | 3 | 3 | 0,129 |
| Becker, 1992 | Reduviidae | multi | 1 | 3 | 3 | 0,873 |
| Becker, 1992 | Phymatidae | multi | 1 | 3 | 3 | 0,498 |
| Becker, 1992 | Lygaeidae | multi | 1 | 3 | 3 | 0,775 |
| Becker, 1992 | Pentatomidae | multi | 1 | 3 | 3 | 0,657 |
| Becker, 1992 | Tingidae | multi | 1 | 3 | 3 | -0,213 |
| Becker, 1992 | Piesmatidae | multi | 1 | 3 | 3 | 0,331 |
| Becker, 1992 | Berytidae | multi | 1 | 3 | 3 | 0,603 |
| Becker, 1992 | Pyrrhocoridae | multi | 1 | 3 | 3 | 0,772 |
| Becker, 1992 | Coreidae | multi | 1 | 3 | 3 | 0,601 |
| Becker, 1992 | Reduviidae | multi | 1 | 3 | 3 | 0,643 |
| Becker, 1992 | Phymatidae | multi | 1 | 3 | 3 | -0,231 |
| Becker, 1992 | Lygaeidae | multi | 1 | 3 | 3 | 0,784 |
| Becker, 1992 | Pentatomidae | multi | 1 | 3 | 3 | 0,877 |
| Becker, 1992 | Tingidae | multi | 1 | 3 | 3 | 0,486 |
| Becker, 1992 | Piesmatidae | multi | 1 | 3 | 3 | 0,796 |
| Becker, 1992 | Berytidae | multi | 1 | 3 | 3 | 0,718 |
| Becker, 1992 | Pyrrhocoridae | multi | 1 | 3 | 3 | -0,211 |
| Becker, 1992 | Coreidae | multi | 1 | 3 | 3 | 0,709 |
| Becker, 1992 | Phymatidae | multi | 1 | 3 | 3 | -0,020 |
| Becker, 1992 | Lygaeidae | multi | 1 | 3 | 3 | 0,801 |
| Becker, 1992 | Pentatomidae | multi | 1 | 3 | 3 | 0,635 |
| Becker, 1992 | Tingidae | multi | 1 | 3 | 3 | 0,150 |
| Becker, 1992 | Piesmatidae | multi | 1 | 3 | 3 | 0,238 |
| Becker, 1992 | Berytidae | multi | 1 | 3 | 3 | 0,186 |
| Becker, 1992 | Pyrrhocoridae | multi | 1 | 3 | 3 | 0,822 |
| Becker, 1992 | Coreidae | multi | 1 | 3 | 3 | -0,415 |
| Becker, 1992 | Reduviidae | multi | 1 | 3 | 3 | -0,361 |
| Becker, 1992 | Phymatidae | multi | 1 | 3 | 3 | -0,241 |
| Becker, 1992 | Lygaeidae | multi | 1 | 3 | 3 | -0,195 |
| Becker, 1992 | Pentatomidae | multi | 1 | 3 | 3 | -0,370 |
| Becker, 1992 | Tingidae | multi | 1 | 3 | 3 | 0,214 |
| Becker, 1992 | Piesmatidae | multi | 1 | 3 | 3 | 0,120 |
| Becker, 1992 | Berytidae | multi | 1 | 3 | 3 | 0,853 |
| Becker, 1992 | Pyrrhocoridae | multi | 1 | 3 | 3 | 0,873 |
| Becker, 1992 | Coreidae | multi | 1 | 3 | 3 | 0,446 |
| Becker, 1992 | Reduviidae | multi | 1 | 3 | 3 | 0,743 |
| Becker, 1992 | Phymatidae | multi | 1 | 3 | 3 | 0,743 |
| Becker, 1992 | Lygaeidae | multi | 1 | 3 | 3 | -0,174 |
| Becker, 1992 | Pentatomidae | multi | 1 | 3 | 3 | 0,757 |
| Becker, 1992 | Tingidae | multi | 1 | 3 | 3 | 0,761 |
| Becker, 1992 | Piesmatidae | multi | 1 | 3 | 3 | 0,415 |
| Becker, 1992 | Berytidae | multi | 1 | 3 | 3 | 0,760 |
| Becker, 1992 | Pyrrhocoridae | multi | 1 | 3 | 3 | 0,254 |
| Becker, 1992 | Coreidae | multi | 1 | 3 | 3 | 0,917 |
| Becker, 1992 | Reduviidae | multi | 1 | 3 | 3 | 0,554 |
| Becker, 1992 | Phymatidae | multi | 1 | 3 | 3 | 0,415 |
| Becker, 1992 | Lygaeidae | multi | 1 | 3 | 3 | 0,760 |
| Becker, 1992 | Pentatomidae | multi | 1 | 3 | 3 | 0,792 |
| Becker, 1992 | Tingidae | multi | 1 | 3 | 3 | 0,736 |
| Becker, 1992 | Piesmatidae | multi | 1 | 3 | 3 | -0,060 |
| Becker, 1992 | Piesmatidae | multi | 1 | 3 | 3 | 0,249 |

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|--|-----------------------|-----------------------|--------|----|---|---|---|--------|------------------|------------------|
| Nilsson et al., 1988 and Bengtsson et al., unpubl. & Holt et al. 1999 | Land snails | Spiders | 0,197 | 17 | 1 | 4 | 3 | forest | temperate | Sweden |
| Nilsson et al., 1988 and Ahlén et al., 1982 | Woody plants | Birds | -0,238 | 17 | 1 | 4 | 3 | forest | temperate | Sweden |
| Nilsson et al., 1988 Bengtsson et al., unpubl. & Holt et al., 1999, and Ahlén et al., 1982 | Woody plants | Spiders | -0,568 | 17 | 1 | 5 | 2 | forest | temperate | Sweden |
| Ricklefs et al., 1999 | Birds | Birds | 0,204 | 17 | 1 | 4 | 3 | forest | temperate | Sweden |
| Ricklefs et al., 1999 | Birds | Bats | 0,280 | 17 | 2 | 3 | 3 | tropic | Lesser Antilles | Lesser Antilles |
| Ricklefs et al., 1999 | Birds | Reptiles & amphibians | -0,005 | 19 | 2 | 3 | 3 | tropic | Lesser Antilles | Lesser Antilles |
| Ricklefs et al., 1999 | Birds | Butterflies | 0,540 | 15 | 2 | 4 | 3 | tropic | Lesser Antilles | Lesser Antilles |
| Ricklefs et al., 1999 | Bats | Reptiles & amphibians | 0,165 | 17 | 2 | 3 | 3 | tropic | Lesser Antilles | Lesser Antilles |
| Ricklefs et al., 1999 | Bats | Butterflies | 0,271 | 15 | 2 | 4 | 3 | tropic | Lesser Antilles | Lesser Antilles |
| Ricklefs et al., 1999 | Reptiles & amphibians | Butterflies | 0,451 | 15 | 2 | 4 | 3 | tropic | Lesser Antilles | Lesser Antilles |
| Roos et al., 2004 | Annonaceae | Lauraceae | 0,310 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Annonaceae | Urticaceae | -0,798 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Annonaceae | Anacardiaceae | 0,206 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Annonaceae | Podocarpaceae | -0,542 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Annonaceae | Dipterocarpaceae | 0,523 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Annonaceae | Euphorbiaceae | -0,920 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Annonaceae | Fagaceae | 0,558 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Annonaceae | Meliaceae | 0,193 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Annonaceae | Myristicaceae | 0,811 | 6 | 3 | 1 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Annonaceae | Araceae | 0,267 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Annonaceae | Rosaceae | -0,432 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Annonaceae | Nepenthaceae | 0,156 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Annonaceae | Cunoniaceae | -0,724 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Annonaceae | Boraginaceae | -0,544 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Annonaceae | Loranthaceae | -0,390 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Annonaceae | Mimosaceae | -0,759 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Annonaceae | Polypodiaceae | -0,673 | 6 | 3 | 3 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Annonaceae | Sapindaceae | -0,541 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Annonaceae | Caesalpiniaceae | 0,204 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Annonaceae | Urticaceae | 0,245 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Annonaceae | Anacardiaceae | 0,987 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Annonaceae | Podocarpaceae | -0,177 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Lauraceae | Dipterocarpaceae | 0,871 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Lauraceae | Euphorbiaceae | -0,033 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Lauraceae | Fagaceae | 0,465 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Lauraceae | Meliaceae | 0,954 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Lauraceae | Myristicaceae | -0,080 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Lauraceae | Cunoniaceae | -0,549 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Lauraceae | Boraginaceae | -0,827 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Lauraceae | Loranthaceae | -0,282 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Lauraceae | Mimosaceae | -0,741 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Lauraceae | Polypodiaceae | 0,136 | 6 | 3 | 3 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Lauraceae | Sapindaceae | -0,860 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |
| Roos et al., 2004 | Lauraceae | Caesalpiniaceae | 0,440 | 6 | 3 | 2 | 1 | tropic | Malesian islands | Malesian islands |

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|-------------------|---------------|------------------|--------|---|---|
| Roos et al., 2004 | Urticaceae | Anacardiaceae | 0,368 | 3 | 6 |
| Roos et al., 2004 | Urticaceae | Podocarpaceae | 0,173 | 3 | 6 |
| Roos et al., 2004 | Urticaceae | Dipterocarpaceae | 0,096 | 3 | 6 |
| Roos et al., 2004 | Urticaceae | Euphorbiaceae | 0,950 | 6 | 3 |
| Roos et al., 2004 | Urticaceae | Fagaceae | -0,053 | 6 | 3 |
| Roos et al., 2004 | Urticaceae | Meliaceae | 0,416 | 6 | 3 |
| Roos et al., 2004 | Urticaceae | Myristicaceae | -0,960 | 6 | 3 |
| Roos et al., 2004 | Urticaceae | Araceae | 0,231 | 6 | 3 |
| Roos et al., 2004 | Urticaceae | Rosaceae | 0,296 | 6 | 3 |
| Roos et al., 2004 | Urticaceae | Nepenthaceae | 0,197 | 6 | 3 |
| Roos et al., 2004 | Urticaceae | Cunoniaceae | 0,217 | 6 | 3 |
| Roos et al., 2004 | Urticaceae | Boraginaceae | 0,173 | 6 | 3 |
| Roos et al., 2004 | Urticaceae | Loranthaceae | 0,471 | 6 | 3 |
| Roos et al., 2004 | Urticaceae | Mimosaceae | 0,440 | 6 | 3 |
| Roos et al., 2004 | Urticaceae | Polyodiaceae | 0,909 | 6 | 3 |
| Roos et al., 2004 | Urticaceae | Sapindaceae | -0,011 | 6 | 3 |
| Roos et al., 2004 | Urticaceae | Caesalpiniaceae | 0,315 | 6 | 3 |
| Roos et al., 2004 | Urticaceae | Podocarpaceae | -0,213 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Dipterocarpaceae | 0,870 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Euphorbiaceae | 0,102 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Fagaceae | 0,498 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Meliaceae | 0,973 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Myristicaceae | -0,199 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Araceae | 0,468 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Rosaceae | -0,533 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Nepenthaceae | 0,777 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Cunoniaceae | -0,536 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Boraginaceae | -0,727 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Loranthaceae | -0,135 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Mimosaceae | -0,629 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Polyodiaceae | 0,253 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Sapindaceae | -0,812 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Caesalpiniaceae | 0,523 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Dipterocarpaceae | -0,626 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Euphorbiaceae | 0,266 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Fagaceae | -0,953 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Meliaceae | -0,326 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Myristicaceae | -0,111 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Araceae | -0,910 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Rosaceae | -0,359 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Nepenthaceae | 0,262 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Cunoniaceae | 0,884 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Boraginaceae | -0,013 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Loranthaceae | -0,515 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Mimosaceae | 0,105 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Polyodiaceae | -0,094 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Sapindaceae | 0,421 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Caesalpiniaceae | -0,866 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Euphorbiaceae | -0,182 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Fagaceae | 0,829 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Meliaceae | 0,916 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Myristicaceae | -0,018 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Araceae | 0,745 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Rosaceae | -0,318 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Nepenthaceae | 0,568 | 6 | 3 |
| Roos et al., 2004 | Anacardiaceae | Cunoniaceae | -0,881 | 6 | 3 |

