

Estimating species richness through three dimensions

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Abstract. Extrapolation techniques allow more accurate estimates of species richness than are possible through simple species counts alone. Similarly, sampling through three dimensions in dimensionally complex ecosystems gives more reliable estimates of species richness and diversity than samples taken at only one level. This paper examines three-dimensional spatial patterns of Coleoptera in primary rainforest in Sulawesi (Indonesia) and demonstrates how adding extra levels in a sampling area (i.e. volume) significantly increases estimated species richness. Evidence for stratification of assemblages at different heights is also examined. Implications for species-area relationships (SARs) are discussed, and how such sampling and extrapolation techniques may impact species-richness measurements in derived ecosystems.

Keywords: disturbance, flying insects, island biogeography, rainforest, SAR, SVR, vertical stratification

INTRODUCTION

Habitat loss, fragmentation and degradation are major threats to global biodiversity (Laurance & Bierregaard 1997), especially in rainforest which may contain approximately half of all species (Dirzo & Raven 2003). Around 1 million of *ca.* 1.9 million described species are insects (Chapman 2009): clearly research into the effects of environmental disturbance on insect diversity, in particular those in rainforest, will play a major role in understanding the impact of human disturbance on natural systems.

The species-area relationship SAR (Preston 1960, 1962a, 1962b; MacArthur & Wilson 1963; Connor & McCoy 1979; see review in Davis & Sutton 2011) describes the increase in species richness with increasing sample area, and has been described as the closest thing to a law in ecology (Lawton 1999). Numerous models have been developed to represent SARs over many years (Whittaker & Triantis 2012), each examining the fit of data to species-area curves and developing respective explanatory theories of species diversity (Connor & McCoy 1979; Scheiner 2003, 2004, 2009; Tjørve 2003; Triantis *et al.* 2008; Dengler 2009; Guilhaumon *et al.* 2010; Santos *et al.* 2010). The earliest model, developed by Arrhenius (1921) and summarized by Preston (1962a, 1962b), known as the power law, takes the form $S = cA^z$, where

S is species richness, A is area, and c and z are constants: z is the slope of the species-area line and c is the point of intersect on the y-axis (when data are plotted on log-log axes). Predictions of biodiversity loss frequently use SARs where associations between species richness and sample area lead to estimations of species loss (Thomas *et al.* 2004).

Sampling regimes have also been shown to affect species-richness patterns (Williamson 2003) and clearly, for data to be as accurate as possible, thorough species sampling is essential. Tropical rainforest in particular provides complex architectural space that allows for extensive niche diversification and speciation: samples in such ecosystems should therefore aim to sample as much of the forest space as possible to ensure comprehensive coverage of species assemblages (see below), in order to investigate possible species-volume relationships (SVRs, *sensu* Davis & Sutton 2011). As well as SVR, other interesting extensions to the SAR concept have been proposed. A temporal analogue of the SAR, the species-time relationship (STR; Rosenzweig 1995) was proposed where species richness increases regularly with the time period of sampling. Adler *et al.* (2005) proposed a species-time-area relationship, or STAR (i.e. considering species number as a function of both the area and time span of sampling), and Storch *et al.* (2005) linked SAR with energy availability (i.e. the effects of productivity on species richness) in species-area-energy relationships (see also Beck *et al.* 2011).

Analysis and discussions presented here follow on from earlier papers examining the spatial distribution of flying beetles caught by light trap in tropical rainforest in Sulawesi, and how these data impact on species-richness measurements (Davis *et al.* 2011, Davis & Sutton 2011), and extends the discussion to the use of species-richness estimates in establishing meaningful calculations of biodiversity extent and species loss.

Davis *et al.* (2011) presented data, collected using aerial traps forming a vertical transect, that gave a clear indication of beta-diversity in the vertical dimension, showing turnover in taxa from the forest floor to the canopy, with concentration of species richness and specificity to any given level being much greater in the canopy. Analysis of the Sulawesi beetle data showed a 50% increase in species count for every additional 10 m of vertical height sampled – this led to conclusions that SVRs may be a more appropriate measure of species richness than area (Davis & Sutton 2011). Although Davis & Sutton (2011) put forward the ‘50% increase’ as an observation rather than a rule, it would clearly be useful to ascertain whether there is a general relationship between height sampled and species-richness increase which could then be applied to SARs. If the 50% increase for every 10 m added vertically is to be generally applicable, stratification of beetle assemblages would have to be seen at each level sampled (in this study, 1 m or ground, 10 m, 20 m and 30 m): analysis showed specializations at both ground and canopy levels, with the highest stratum preference shown in the canopy (Davis *et al.* 2011). Here we examine whether there is evidence for stratum preference in the mid-levels of the forest, and whether the 50% rule may be generally applicable, although we recognize that results presented here represent only one guild, i.e. flying beetles caught by light trap, and that such a generalization is problematic, even if the beetle samples represent a sizeable portion of the biodiversity at the site (see Discussion).

We also examine whether estimated species richness (i.e. estimates of the full assemblage species richness, calculated using extrapolation techniques from data presented in Davis *et al.* 2011), follows the same pattern as that shown in Davis & Sutton (2011), and the implications that such measures may have on the calculation and interpretation of SARs in primary and derived ecosystems.

MATERIALS & METHODS

Beetles were collected from a primary rainforest site surrounding the Morowali Walkway Camp of Operation Drake (1980-1981) in Central Eastern Sulawesi (Sulawesi Tengah). A vertical transect of four actinic traps was positioned from one semi-emergent *Syzygium syzygioides* (Miq.) Merrill & Perry. The levels used were 1 m, 10 m, 20 m, and 30 m. The 30 m and 20 m traps were located in the contiguous leaf layer of the upper canopy, with the 30 m trap located within the crown of the *Syzygium* (Myrtaceae) and the 20 m trap was *ca.* 2 m above the crown of a *Garcinia* species (Guttiferae). The 10 m trap was at least 5 m clear of any foliage and located in free space. The traps were operated continuously from 19.00 to 22.00 hours between 14 February and 16 March 1980, and for trial periods before and after these dates.

The four traps were run simultaneously so as to reduce the possibility of movement up or down the column: this would have been a problem had traps at different heights been run at different times. Moth studies have shown that light traps only sample from the immediate vicinity of the trap (Truxa & Fiedler 2012) and so there is likely to be little interference between traps as range of influence is limited (see also Davis *et al.* 2011). Morphospecies identification was exhaustively carried out at the Natural History Museum, London (for details see Davis *et al.* 2011).

Different methods exist for estimating species richness from samples (Colwell & Coddington 1994; see Magurran 2007 for overview). Parametric methods fit data to species-abundance distributions, generally either log-series or log-normal, which then allow for total species richness in the community to be estimated. If data do not fit specific species-abundance distributions then calculations are invalid. Log-series distributions predict that the largest class will be represented by one individual and estimates therefore increase as the number of individuals sampled rises, and log-normal distribution estimates often prove problematic as they are affected by the degree to which part of the community remains unsampled (i.e. the area in the distribution curve behind the veil line – Magurran 2007).

Nonparametric estimators, which are not based on the parameter of a species abundance model that has previously been fitted to the data, have proven to be more effective and powerful than other methods (Magurran 2007; see also Beck & Schwanghart 2010, for further comparisons of species diversity from incomplete inventories). Two such extrapolation methods, Chao 1 and Chao 2 (Colwell & Coddington 1994), use different properties of the species assemblage to estimate richness. Chao 1 estimates total richness as $S + a^2/2b$ where a is the number of singletons in the total sample and b is the number of doubletons. Chao 2 uses incidence data rather than abundance data, where a (using the same equation as above) is the number of species occurring in only one sample and b the number occurring in only two. These

estimators give a robust method for estimating unsampled species that are then added to the total species count. Here we use Chao 1 as the primary means of estimating total species richness of beetles within the assemblage. For comparative purposes, we also calculate other species-richness estimates using other nonparametric methods: Chao 2 (see above), ACE (abundance-based coverage estimator), Jackknife 1, and Jackknife 2 (Chao *et al.* 2000, Colwell 2005). Confidence limits can be calculated for many of these estimators (Colwell 2005). Although many of these species-richness estimators assume homogeneity among samples, which cannot be assumed along environmental gradients, application of estimators on larger geographic scales (hence containing non-random heterogeneity) suggests that the approach presented here is valid (Mora *et al.* 2011).

The extent to which middle levels of the vertical column sampled contribute to overall diversity, and therefore the degree to which stratum preference may exist at these levels, were examined by pooling samples – ground and canopy (traps 1 and 4) and mid-levels (traps 2 and 3) – and estimating species richness (Chao 1) and Fisher's alpha (Magurran 2007) from these samples. The closer values from canopy and ground pooled samples are to those from the full sample, the less the contribution from the middle levels is likely to be. The number of species found only at one level was also counted, to give an indication of stratum preferences, although undersampling will lead to an overestimation of stratum preference (J. Beck, pers. comm.).

Species-richness estimates were calculated using EstimateS (Version 8.2), Colwell (2005).

RESULTS

Collections over the 1-month sampling period resulted in 11,692 specimens representing 701 species (Davis *et al.* 2011). Extrapolation techniques applied to sample data provided a variety of species-richness estimates (see Materials & Methods). Results for Chao 1 for each level are shown in Table 1. Table 1 also gives values for alpha-diversity at each level, and accumulative values for combined samples from ground to canopy. Chao 1 predicts the richness in terms of actual species numbers whereas alpha merely gives a measure of relative richness. Table 2 shows accumulative Chao 1 estimates from ground to canopy using combined sample data: accumulative estimated species richness was calculated as a function of height by summing the estimated number of species found at each height in turn – these data are shown in Table 2 as *acc. ES* (accumulative estimated species richness). Table 2 also gives accumulative numbers of singletons and doubletons, and the ratio of species richness at consecutive heights (*acc. ES ratio*), calculated by dividing the accumulative estimated species richness at each height by the value of the level below.

Table 1. Total number of individuals (N), species richness (S), diversity (Fisher's alpha, α), accumulative diversity measures for pooled samples ($acc. alpha$) and estimated species richness (ES) for assemblages of Coleoptera at different heights in rainforest in Sulawesi, and for total sample.

height (m)	N	S	Fisher's alpha		Chao 1
			α	$acc. alpha$	ES
1	1,571	224	71.45	-	453
10	2,108	256	76.33	99.55	483
20	2,964	324	92.68	121.71	596
30	5,049	464	124.42	163.69	847
total	11,692	701	163.69	-	1,298

Notes:

total = calculations for total sample.

$acc. alpha$ values calculated by pooling samples consecutively from 1 to 30 m: value for 30 m is therefore the same as Fisher's alpha for the total sample (all heights combined).

Table 2. Accumulative species richness and accumulative estimated species richness of Coleoptera against trap height in tropical rainforest in Sulawesi.

height (m)	$acc. N$	$acc. S$	$acc. single$	$acc. double$	$acc. ES$	- 95%	+ 95%	$acc. ES ratio$
1	1,571	224	123	33	453	363	602	-
10	3,679	362	181	55	660	561	809	1.46
20	6,643	489	217	84	769	685	890	1.17
30	11,692	701	326	89	1,298	1,139	1,514	1.69

Notes:

$acc. N$ = accumulative number of individuals; $acc. S$ = accumulative species richness from ground to canopy (see Davis & Sutton 2011); $acc. single$ = accumulative number of singletons in assemblage; $acc. double$ = accumulative number of doubletons in assemblage; $acc. ES$ = accumulative estimated species richness from ground to canopy (estimated species richness calculated using Chao 1, see Materials & Methods); - 95% = lower boundary of log-linear confidence interval; + 95% = upper boundary of log-linear confidence interval (Colwell 2005); $acc. ES ratio$ = increase in estimated species richness as a proportion of ES at previous height (accumulative species ratio).

In addition to Chao 1, other richness estimates were calculated. Chao 2 for the full sample (i.e. all forest levels) = 1,408 (log-linear confidence interval lower bound = 1,238, log-linear confidence interval upper bound = 1,632); ACE = 1,170; Jackknife 1 = 1,005; Jackknife 2 = 1,169.

Species-richness estimates were calculated for combined levels (1 and 4, 2 and 3 – see Material & Methods). Combined canopy and ground samples resulted in Chao 1 = 991 ($N = 6,620$; $S = 551$; no. singletons = 257, 47% of sample; no. doubletons = 75, 14% of sample), and combined mid-levels (samples 2 and 3) resulted in Chao 1 = 683 ($N = 5,072$; $S = 415$; no. singletons = 188, 45% of sample; no. doubletons = 66, 16% of sample). Overall therefore the canopy and ground traps contained a greater proportion of the total estimated sample (all forest levels combined) than the mid-level samples (see Discussion).

Species only sampled at one height were counted – of these the majority were either singletons or doubletons, with only the canopy containing larger abundances of unique species. The number of species recorded at only one height is as follows: 1 m = 59 species (3 of which had > 2 individuals; with none containing > 10 individuals), 10 m = 55 species (> 2 = 1; > 10 = 1), 20 m = 78 species (> 2 = 1; > 10 = 0), and 30 m = 212 species (> 2 = 22; > 10 = 5).

DISCUSSION

This study clearly shows a significant element of beta-diversity from ground to canopy as indicated by the values of Fisher's alpha up the column with a distinct increase up to the canopy (Table 1, Table 2). The highest value (in the canopy sample) is significantly exceeded by the alpha value for the total sample, which along with the incremental increase is an indication of the presence of beta-diversity in the vertical dimension.

Table 1 also shows estimated species-richness values for each level and the pooled sample: these values almost show a linear relationship with each other and with S , indicating both turnover in the column and an additive effect from pooling, and also that undersampling has probably not been a problem. All values for estimated species richness show general conformity, ranging from 1,005 (Jackknife 1) to 1,408 (Chao 2) with a mean estimate of 1,210 species in the full sample. All estimates considerably increase values for species richness from raw sample data, and this, combined with the significant element of beta-diversity up the column, clearly indicates that raw species-richness measurement taken from only one level of an ecosystem may seriously underestimate overall species richness.

The beetle data from Sulawesi show that species-richness counts increase as samples are progressively pooled from ground to canopy (Davis & Sutton 2011), and that estimates of species richness repeat this pattern to even more pronounced effect (Table 2). Most studies of SARs use actual species counts rather than estimated richness values (Triantis *et al.* 2012). Whilst measurements of species richness for larger animals (e.g. mammals and birds) may be relatively reliable, this is unlikely to be the case for smaller animals (Coddington *et al.* 2009). Data presented here suggest that extrapolation techniques should be used to estimate more accurately the total species richness in an area, especially when studying small animals such as insects. The message for SARs would appear to be clear: data used in SAR analysis should use estimated richness for taxa where it is unlikely that all species have been collected (e.g. insects), sampled from the full vertical extent.

Data were originally analysed to examine stratification at canopy and ground levels, to allow comparison with other studies (Stork & Grimbacher 2006) and did not otherwise differentiate whether turnover up the vertical column was a continuum or whether there was true stratification of species at all levels, with clumping of species distributions in the mid-levels. Over half of the more abundant species were distributed over the whole column, but significant preference or specialism for middle levels was not detected. The observation that there was a 50% increase in species richness per 10 m vertically (Davis & Sutton 2011) was used to emphasize the effect of sampling through three dimensions has on species-richness measures, with the concomitant effects on SARs. If this observation is to be widely applicable then assessment of the structure of turnover up the column is critical: if there is no specialism and enrichment at middle levels then it is questionable whether this relationship will hold with greater 'trunk length' of trees. Comparison with other insect groups is also necessary.

A species-richness estimate for pooled canopy and ground data showed 76% of the total sample (all levels) estimate, whereas pooled mid-levels indicated only 53% of the total pooled sample estimate, indicating that less stratification exists in the mid-levels compared to canopy and ground. Species found at only one level showed a similar pattern at each level (see Results), with only the canopy stratum showing high levels of specialization (see also Davis *et al.* 2011). Overall, 65% of the estimated richness is present in the canopy sample, but only 35% is present in the ground level sample (Table 1). In addition, the accumulative estimated species-richness (Chao 1) measures do not follow a linear pattern, with a tailing off at 20 m (Table 2), with the canopy paying a greater role in contributing to total estimated species richness than was shown by the raw data: again, this suggests less stratification in mid-layers. Although the average increase in estimated species richness between levels is 44%, similar to that shown by species-richness measures, the pattern of increase differs, with only a 17% increase at 20 m. The linear species-increment pattern seen in this study (Davis & Sutton 2011) may therefore not hold in forests with greater trunk length: clearly there is much scope here for further study. Measurements from forests of lower or higher stature would enable assessment of whether a more elevated canopy leads to more species being able to pack in at lower levels, and whether greater proximity of canopy and understorey in less lofty forests compresses effects of competition, resulting in fewer species being able to coexist. The Sulawesi forest is unusual in often having a dominance of palms, particularly rattans, in the understorey relative to forests of other islands such as those on the Sunda Shelf or New Guinea. Comparative studies are needed to examine patterns.

In addition to variation in forest structure, the distribution of different insect groups may vary: a vertical component of beta-diversity in forest insects has been shown but responses can

differ (see review in Davis *et al.* 2011). Kato *et al.* (1995) showed that Lepidoptera numbers in tropical rainforest in Borneo, Malaysia, were evenly distributed from ground to canopy, beetle numbers increased significantly from floor to canopy, and Hemiptera were very much more abundant in the canopy than at the other levels, and that patterns mirrored those seen in Sulawesi (Sutton 1983). The total species richness of flying Coleoptera presented here was 2.86 times that of the bottom trap alone (Chao 1 figures – Table 1): this contrasts with Lepidoptera data from Malaysia, where Holloway & Intachat (2003) showed that the total richness was only 1.36 times that of the bottom trap, and Willott (1999) demonstrated that total canopy and understorey samples pooled together were only 1.32 times as rich as the latter alone. Studies from South-east Asia therefore indicate that (a) different insect groups seem to show similar vertical profiles in Sulawesi and Malaysia, and that (b) these differ markedly from group to group (Sutton 1983, Kato *et al.* 1995, Willott 1999, Holloway & Intachat 2003). Beetles, possibly because of the greater diversity in their trophic requirements, show perhaps the most significant vertical turnover and beta-diversity, but this does not necessarily translate into a general incremental rule up the vertical column for all groups (J. Holloway, pers. comm.). Again, comparative data would be welcome to investigate the nature of stratification in complex ecosystems, and the way this impacts on SVRs.

Spatial scaling is an important organizing principle of biogeographical patterns (Whittaker 2000). The influence of aspects such as vegetation height and geographical relief (which may also affect SARs – Davis & Sutton 2011) may decrease with increase of scale to the point where area becomes a satisfactory surrogate for assessing diversity in all processes within gross life-zones, and it remains to be seen what effect spatial scale may have on SVRs.

Recent analysis of how well different SAR models fit available data showed that simpler models performed best, with the power law (see Introduction) ranked first (Triantis *et al.* 2012). Early formulations of the power law SAR model used emigration and immigration patterns to describe species-richness patterns (MacArthur & Wilson 1963), but more recent studies have used speciation and evolutionary processes to augment patterns and explain underlying trends (Heaney 2000, Losos & Schluter 2000, Drakare *et al.* 2006, Kisel *et al.* 2011, Rosindell & Phillimore 2011). The correlation between forest structural diversity and taxonomic diversity has long been established (Southwood *et al.* 1979). Clearly, in tropical rainforest and other dimensionally rich ecosystems, speciation may play a major role in determining species-richness distributions and therefore impact SAR models, and such a process is certainly frequent in Sulawesi insect groups, as illustrated by Holloway (1991, 2003) for the Lepidoptera. The environmental gradient that exists from ground to canopy provides an axis through which sympatric speciation can take place (Schilthuizen 2001). Populations can more easily become specialized to different habitats along steep environmental gradients (e.g. ground to canopy) and in heterogeneous ecosystems, making speciation more likely and perhaps more rapid (Schluter 2009). Such factors may increase the slopes (z variable) and intercepts (c variable) of SARs. Drakare *et al.* (2006) showed higher z -values and therefore steeper SAR slopes in forested areas compared to non-forested, and between marine (high slope) and lake (low slope) ecosystems, and suggested that this may be related to higher vertical

dimensions in forest and seas compared to non-forested areas and lakes allowing more rapid species turnover and so steeper SAR. Davis & Sutton (2011) suggested that undersampling insect assemblages may also affect parameters of the power law SAR. Given the enhanced species-richness measures provided using the extrapolation techniques outlined in this paper, in addition to the species turnover noted from canopy to ground, it is likely that effects on the power law parameters could be very pronounced indeed and both factors need to be taken into account in SARs.

Human-dominated ecosystems currently constitute 75% of the global land surface (Ellis *et al.* 2010) and so it is essential that SAR research is applied accurately in modified ecosystems (Mendenhall *et al.* 2012). SARs have been used to estimate species extinction, identify biodiversity hotspots, and provide a workable tool for conservation planning, although interpretations of such data remain contentious (Guilhaumon *et al.* 2008, Smith 2010, He & Hubbell 2011, Fattorini & Borges 2012, Thomas & Williamson 2012). Any effects of sampling and species-richness measurement on the parameters of SAR models, as discussed above, will have knock-on effects for the accuracy of these models in predicting biodiversity loss. Again, we suggest that sampling must include all levels of the ecosystem, with species-richness estimates being used rather than simple species counts.

As well as habitat area, other factors can also affect species survival such as edge effects induced by habitat fragmentation and disturbance (Laurance 2008). Simple species counts may hide differences in community composition between habitat types, with associated implications for ecosystem functioning (Mendenhall *et al.* 2012). Studies on insects in disturbed tropical forests have shown vertical compression of beta-diversity through proliferation of edge effects, with canopy species being sampled nearer to the ground, leading to enhanced species richness in ground traps (Davis & Sutton 1998, Willott 1999, Davis *et al.* 2001, Fermon *et al.* 2005, Tregidgo *et al.* 2010). There is a danger that studies of species richness taken from ground traps only will lack an appreciation of species turnover from ground to canopy, leading to an inappropriate use of data in SAR analysis (i.e. underestimate the diversity in primary forest, and overestimate species richness in derived ecosystems). Once again, these studies show the necessity of encompassing the spatial heterogeneity of the forest in sampling regimes, and include the canopy in any attempt to monitor the effects of disturbance on forest assemblages.

CONCLUSIONS

Data presented here show the effect of sampling and extrapolation techniques on total species-richness measures. Samples taken from ground level recorded only 224 species, whereas 701 species were recorded from all heights of the forest, and this figure was increased further when extrapolation techniques were used to estimate total species count (a mean estimate of 1,210 species). Even once the effects of spatial scaling have been taken into account (i.e. samples taken from a larger area of forest than possible in this study) raw species counts taken from only one layer of the forest (i.e. the ground) are likely to seriously

underestimate total species richness. SARs make the assumption that species counts are comprehensive, but can this supposition be justified? Species counts for small and spatially heterogeneous animals such as insects are likely to be less reliable than those for larger and more highly visible animals (e.g. mammals and birds). We suggest that using species-richness estimates, as well as employing vertical and horizontal sampling regimes, would result in more rigorous data for analysing species distribution patterns and processes.

ACKNOWLEDGEMENTS

Our thanks to taxonomists who made analysis of the Sulawesi beetle data possible (see Davis *et al.* 2011). This paper was instigated following correspondence with Jeremy Holloway, whose subsequent thoughts and comments greatly added to its content. Our thanks also to Jan Beck for insightful and helpful comments on an earlier version of the paper, and to Chey Vun Khen for carefully checking the manuscript prior to publication.

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