

Species-volume relationships in tropical rainforests

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Abstract. Island biogeography theory relates species richness to habitat area. This paper suggests that using two-dimensional area measurements in three-dimensionally complex ecosystems does not give reliable estimates of species richness or diversity, and that volume measurements should be used, especially when studying organisms that have fine-grained niche requirements such as arthropods. 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 the measure of species richness. A linear relationship exists that shows a 50% increase in species richness for every 10 m added to a vertical transect. A review of the literature is made in light of these observations. Implications regarding the measurement of species richness in complex ecosystems are discussed and possible repercussions on the estimation of species extinction following habitat disturbance.

Keywords: habitat complexity, heterogeneity, island biogeography, SAR, species richness, SVR

INTRODUCTION

When Preston (1962a, 1962b) summarized the work of Arrhenius (1921) in the equation

$$S = cA^z,$$

he described what has come to be known as the species-area relationship (SAR). In so doing, he formed the basis for a more quantitative, theoretical and predictive foundation for ecology. In this paper, we describe the extension of this concept to species-volume relationships (SVR). In the species-area, or 'Arrhenius' equation (Preston 1962a, 1962b), the number of species (S) within an area is related to the size of that area (A) according to the constants c and z , where z is the slope of the species-area line (when data are plotted on log-log axes) and c is the point of intersect on the y-axis. Both z and c are determined by the nature of the organism and the landscape being studied. The equation formed the basis for the seminal work of MacArthur & Wilson (1963, 1967), who expanded the mathematical basis for the species-area relationship to

incorporate isolation, immigration and emigration, and noted that the theory could be applied to continental as well as insular biotas (i.e. continental landmasses can be seen as being made up of habitat islands). Although some early examination of the models with empirical data seemed persuasive, other studies suggested that habitat diversity is a better predictor of species richness than area alone (Williams 1943, 1964). Allied to the habitat-model is the species-energy hypothesis (Hutchinson 1959, Brown 1981, Kerr & Packer 1997) where species richness is limited by proportioning available energy among species in a given locality, and where the primary productivity of an area is correlated to species richness (Wright 1983). The debate over which mechanism is more important (i.e. the area itself, or habitat diversity) has proceeded from the early work to the present time (see summary in Triantis *et al.* 2003, Whittaker & Fernández-Palacios 2007). More recently, an attempt to mesh both mechanisms in one overarching model has been proposed in the Choros model (Triantis *et al.* 2003) which mathematically unites the 'area' (or the 'area *per se*' model, Whittaker & Fernández-Palacios 2007) and 'habitat' models (see Discussion below).

Various proposals have been made for the variation in z in different studies, including the ecology and behaviour of the species in question (e.g. mobility and range size of species, feeding behaviour, etc.), the range of areas sampled, and type of area (i.e. insular vs. continental). Other studies have shown that z varies systematically with climate, for example temperature and precipitation (Kalmar & Currie 2006), and suggest that a new model, combining richness-climate with both SAR (including both area and isolation variables of MacArthur & Wilson's original work 1963, 1967) and species-energy models, is better at predicting species richness than individual models alone (Kalmar & Currie 2006). Predictive models of species richness may require climatic as well as the more traditional variables (Whittaker 2006).

Rainforests have long been seen as hot-spots for biodiversity (Richards 1952), and the insects as the predominant group contributing to this diversity (Erwin 1982, 1991). Vertical stratification of plants and animals in forests is a basic concept in ecology, with the number of strata increasing with decreased latitude (Smith 1973). High habitat heterogeneity is seen as a prime contributor to high diversity, in particular the vertical distribution of insects in these three-dimensionally complex ecosystems. The role of the forest canopy and its contribution to global species richness estimates has been extensively discussed (Erwin 1982, Ødegaard 2000, Stork & Grimbacher 2006), although it is perhaps the gradient of ground to canopy, in both biotic and abiotic variables, that best explains the richness of arthropods in tropical forests. The vertical distribution of insects has been a developing field of study over the last two decades (Sutton 1983, Basset 2001, Basset *et al.* 2003), with improved access to the canopy through modern techniques (see review in Sutton 2001). The importance of habitat volume is well known to tropical entomologists.

Despite the established link between species richness and ecosystem height, through differences in vertical distributions in individual species' niche space, none of the existing predictive species relationship models discusses the volume occupied by species: area is very much the *modus operandi*. Many of the models have volume implicit in their working – for example the greater

the volume of an ecosystem the larger the number of available habitats that can be expected. This paper explores the degree to which volume, rather than area *per se*, is a better descriptor of species richness, especially in three-dimensionally complex ecosystems (e.g. tropical rainforest and coral reef, Connell 1978). One group of highly diverse arthropods – the Coleoptera – is used to investigate species-volume relationships, by examining the vertical distribution of species richness at four levels in lowland tropical rainforest in Sulawesi (Indonesia).

METHODS

Insects were collected from a primary rainforest site surrounding the Morowali Walkway Camp of Operation Drake (1980-1981) in central eastern Sulawesi (Sulawesi Tengah). This area has a tropical monsoon climate with rainfall of about 4,000 mm/yr, with a dry season usually from September to March. The site is described in detail by Rees (1983) and Sutton (1983).

Trapping was carried out using a set of four actinic light traps (Sutton & Hudson 1980) as previously used in Zaire, Brunei, Papua New Guinea, and Panama (Sutton *et al.* 1983). Light trapping does not give a proportional representation of the beetle fauna, but attracts a wide range of taxa very quickly, giving useful sample sizes, and these can be used for comparative purposes. Hammond (1990) compared the effectiveness of various collecting methods on Project Wallace, and rated light trapping as the best along with Malaise trapping, and found that light trapping attracted 87% of the 142 family groups collected by all methods (Hammond 1990).

The traps were suspended at different levels from a semi-emergent *Syzygium syzygioides* (Miq.) Merrill & Perry, which is a common tree in the area. The levels used were 30, 20, 10, and 1 m (which will be referred to here as levels 1-4). Levels 1 and 2 (30 and 20 m) were in the contiguous leaf layer of the upper canopy, whereas levels 3 and 4 were in more open vegetation. The total sample was represented by 27 trap nights from 14 February to 16 March, including trial periods at the beginning and end of the period: here we use data from one lunar month, excluding data from the trial period (following the analysis of Rees 1983), which contain the majority of specimens and all species collected.

The reliability of morphospecies identification is essential if data are to be reliable and comparable with other areas, and the fullest use of 'hands on' knowledge of experts should be made (Hammond 1994). All beetles in the present study were mounted, labelled and sorted to species at the Natural History Museum in London, using the same approach and standards as for the Project Wallace material. The beetles were examined by experts in specific families (see Acknowledgements), thereby increasing the rigour and accuracy of the morphospecies sorting process.

RESULTS

Collections over the 1-month sampling period resulted in 11,692 specimens representing 701 species. Detailed analysis of the spatial patterns are analysed elsewhere (Davis *et al.* 2011). The species richness and number of specimens at each height are shown in Table 1. Accumulative species richness was calculated as a function of height by summing the number of each species found at each height in turn – these data are shown in Table 1 as *acc. S* (accumulative species richness). Figure 1 shows a plot of *acc. S* against trap height – a linear correlation is shown which is significant at $P = 0.05$ ($r = 0.994$, 2 d.f.). The ratio of species richness at consecutive heights was calculated (*acc. S ratio* – Table 1) by dividing the accumulative species at each height by the value of the level below. Between 1 and 10 m, the *acc. S* ratio was 1.62, i.e. there was a 62% increase in the number of species between the two heights. The increase in species richness at the next two heights (20 and 30 m) was 35% and 43% respectively. The mean *acc. S ratio* was 1.47, indicating that a ca. 50% increase in the number of species was recorded for each increase of 10 m in height.

The relationship between species richness and height can be expressed by the equation

$$S = S_i h + c$$

where S = species richness, S_i = species increment (a coefficient measuring incremental species increase, effectively the slope of the correlation), h = height above the ground, and c = the intercept on the y-axis. In this case, $S_i = 16$, and $c = 199$, but both coefficients will vary according to trapping method and organisms studied.

Table 1. Species richness and accumulative species richness of Coleoptera against trap height in tropical rainforest in Sulawesi.

Trap height (m)	N	S	<i>acc. S</i>	<i>acc. S ratio</i>
1	1571	224	224	-
10	2108	256	362	1.62
20	2964	324	489	1.35
30	5049	464	701	1.43

N = number of species; S = species richness; *acc. S* = accumulative species richness from ground to canopy; *acc. S ratio* = increase in species richness as a proportion of S at previous height (accumulative species ratio).

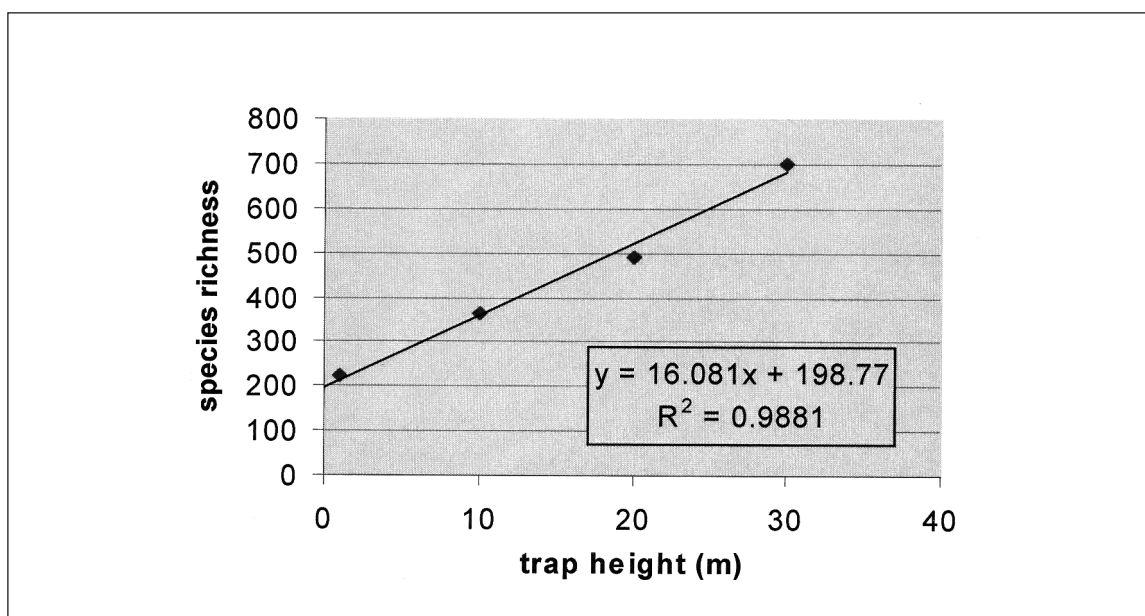


Figure 1. Accumulative species richness of Coleoptera against trap height in tropical rainforest in Sulawesi.

DISCUSSION

The data presented here are based on an exhaustively sorted sample, with RTU (recognizable taxonomic unit) identification at a high level of resolution, and although the lack of replication and small spatial scale must lead to caution, the results are suggestive and indicate various avenues for further research.

In data presented here, for each 1-metre increase in height from ground to canopy there was a 5% increase in species richness – clearly if only a two-dimensional space (i.e. area) had been sampled then the estimates of species richness would have been seriously underestimated. Over three times the number of species was recorded in the sample taken through three dimensions compared to those taken in only two. The literature on predictive modelling of species is based on area measures and not volume, both in terms of the area *per se* models as well as habitat diversity and energy relationships (Drakare *et al.* 2006, and references therein; Whittaker & Fernández-Palacios 2007). We suggest that, in spatially complex ecosystems, habitat volume is a more useful measure than area, as this better reflects habitat heterogeneity, and that poor appreciation of habitat volume may lead to serious flaws in the analysis and interpretation of such species richness data.

Further criticisms of existing models can be made, in addition to those outlined above. The data relating to species richness models show a strong taxonomic and body-size bias towards vascular plants, birds and mammals (Triantis *et al.* 2003), at the expense of smaller more diverse groups such as arthropods and microorganisms, and existing models are therefore biased towards spatial scales much coarser than that experienced by smaller organisms (Drakare

et al. 2006). Where smaller organisms are used, vegetation type tends to be used as a measure of habitat heterogeneity, but not habitat volume (Nilsson *et al.* 1988, Ricklefs & Lovette 1999, Kotz *et al.* 2000, Quin *et al.* 2006). Other limitations of the SAR model have been reviewed elsewhere (Lomolino 2000a, 2000b, 2000c). For example, in many systems, species seldom attain an equilibrium number of species (due to speciation, geological events, or anthropological disturbance) and immigration filters for island ecosystems are not homogenous within or between archipelagos (larger islands may have larger number of habitats; intervening landscapes may differ and affect immigration or emigration in different ways). In natural systems, all species are not equivalent to one another (the MacArthur-Wilson model is species neutral), and different species behave in different and individual ways (Lomolino 2000a, 2000b, 2000c).

Although the *modus operandi* of species richness models varies, e.g. the pattern and ordering of sampling, variation in sample size (the ISAR of Whittaker 2006), and the method of species-area curve classification (Scheiner 2003, 2004), all models use area-relationships rather than volume-relationships, as discussed above. In an attempt to address the area-bias of existing models, Triantis *et al.* (2003, 2005) used a new coefficient K (choros, from a Greek word that describes three-dimensional space) rather than A in the Arrhenius equation, hence forming

$$S = cK^z.$$

In effect, K is a measure of the habitat richness of the study area – clearly if habitat diversity is measured in two-dimensional space then criticism of the area-bias of existing models still applies. The qualification of habitat definition is also a problem in this model and may vary from study to study (Triantis *et al.* 2003).

The current study suggests that species-volume relationships are the most appropriate way to measure species richness and diversity in tropical forests. The concept of species-volume relationships (SVR) is congruent with species-habitat and species-energy relationships, and the proposal of Kalmar & Currie (2006) for an overarching species-area-isolation-climate model: areas with high incident radiation (e.g. the tropics) can expect to have higher net primary productivity and taller vegetation, leading to more vertically complex habitat distribution. The expansion of niche hyperspace into three-dimensionally rich habitat volume gives increased opportunities for sympatric speciation along ecotone gradients (e.g. low light at ground level to high light in the canopy, higher to lower humidity, etc. (August 1983; Davis *et al.* 1997, 2000). Environmental gradients provide the opportunities for speciation (Schilthuizen 2001), especially in groups that show high diversity and fine-grained niche requirements such as arthropods.

The vertical distribution of vertebrates in rainforest is well known (Whitmore 1990). The maintenance of high population densities of congeneric species through the use of three-dimensional home ranges in rainforest has been recorded in animals with larger body size by using vertical as well as horizontal transects (Reagan 1992), and where associations have been made to habitat complexity rather than habitat heterogeneity (August 1983). August (1983) demonstrated the association between habitat complexity (measured by vertical variation in habitat physiognomy) and mammal community structure in tropical forests, but not habitat heterogeneity (measured by horizontal variation in habitat form), indicating that volume plays

the predominant role in shaping mammal communities. We suggest that the bias in SAR studies to larger organisms and (in general) to less complex ecosystems may have underestimated the volume-effects on the diversity and distribution of smaller more diverse groups. If the volume-effects explored here are scale-dependent, studies on taxon groups that are smaller, or that exist in three-dimensionally complex ecosystems, may have in turn resulted in underestimations of the z coefficient. The volume-effects may in part also explain data that do not fit the log-log linear relationship or have z -values that are lower than expected. z -values in terrestrial systems tend to average ca. 0.30 (MacArthur & Wilson 1967, Rosenzweig 1995). Tropical rainforests, if completely sampled both vertically as well as horizontally, could expect to have steeper values of the z coefficient.

Steeper log-log transformed SARs with high z -values have indeed been recorded in coral reef communities, where fish abundance was suggested to be in direct proportion to patch volume causing the SAR to be steeper than in intrinsically two-dimensional systems (Chittaro 2002). Coral reef, like tropical rainforest, is renowned for its spatial complexity and high biodiversity (Connell 1978), and where species-ecosystem relationships are likely to be comparative. High z -values in reef communities, however, have been found to be dependent on random-placement processes (Coleman 1981) which operate at the small spatial scales exemplified by these studies (Belmaker *et al.* 2007), rather than volume-effects, although data may have found a better fit to three-dimensional measurements had they been applied to reef-specific fish (Belmaker *et al.* 2007) where the three-dimensional niche-space provided by the reef could be expected to play a bigger role. It remains to be seen whether volume-effects work at larger spatial scales and for organisms that are distributed along ecotones within the ecosystem volume, and whether they show specific adaptations to the biotic aspects of the system.

The current study shows similarities to work by MacArthur & MacArthur (1961), MacArthur (1972). MacArthur showed that bird species diversity (BSD) was linearly correlated to height profile of foliage density but not to plant species diversity (MacArthur & MacArthur 1961) – an expected pattern as birds are not herbivorous. Subsequent work, in an early niche-partition model, examined the effects of habitat height on species richness, based on bird data, hinting at possible volume relationships (MacArthur 1972). The variable R was used to represent the breadth of the overall habitat dimension (a co-ordinate representing the range of resource subdivided by species), and C (not to be confused with the c -coefficient of the Arrhenius equation) a coefficient that measured the number of neighbours, and that depended on the number of subdivided dimensions. The degree of niche width and overlap between species along the resource co-ordinate and C determined species richness (MacArthur 1972, p. 170). In the current study, R is equivalent to the coefficient h , or height above the ground. MacArthur points out that with vertical as well as horizontal dimensions, constant C increases and so more species can be present (i.e. ‘added geometrical structure gives added dimensionality to the species subdivision’ – MacArthur 1972, p. 179). Our own work showed that for each 1 m increase in height, a 5% increase in species richness resulted (assuming equal attractiveness of the trap at each height), i.e. a doubling of species richness at 20 m (R , or h , = 20), with greatest species richness occurring in the canopy.

The current scale of ecosystem fragmentation and habitat loss is alarming (Reid 1992, Simberloff 1992, Balmford *et al.* 2003), and clearly tools are needed that accurately predict how these changes may lead to loss of biodiversity. SAR has been used as a conservation tool to estimate the effect of fragmentation and habitat loss on species diversity in terrestrial and marine systems (Reid 1992, Lomolino 2000b, Neigel 2003, Thomas *et al.* 2004). For caveats to using SAR as a predictive model of species extinctions, see Ulrich & Buszko (2003) and Lewis (2006). In SAR models all species are treated as alike, and although such synecological approaches provide relatively fast and comprehensive predictions, estimates of species extinctions should ideally be calculated on a species-by-species basis (Simberloff 1992), with endemic species taken into account (Fattorini 2006). Such an autecological approach would inevitably entail complications and problems (Harte *et al.* 2004, Lewis 2006). These approaches have been recommended for understanding and interpreting insect assemblages in tropical forests (Kitching *et al.* 2003). Given the need in many cases for rapid assessment of biodiversity, it is possible that if the z -coefficient is underestimated through incomplete sampling of the habitat volume. If this is the case, then species extinction estimates may also be below true values.

Edge effects, as well as SAR, have been shown to affect species richness following disturbance (Murcia 1995, Didham 1997, Brown & Hutchings 1997, Davis *et al.* 2000, Davis *et al.* 2001, Foggo *et al.* 2001). With the rainforest canopy effectively an edge habitat (Foggo *et al.* 2001), smaller forest fragments will have a higher surface area compared to their volume than larger fragments of equivalent height, and therefore more extensive edge effects – clearly these effects may have serious ramifications for the survival of interior-forest specialists and the proliferation of edge species, and the patterns of species richness in these habitats.

CONCLUSIONS

There is still much debate about SAR (Gould 1979, He & Legendre 1996, Plotkin *et al.* 2000, Whittaker 2000, Connor & McCoy 2001, Lomolino & Weiser 2001, Williamson *et al.* 2001, Lomolino 2002, Matter *et al.* 2002; see summary in Schoereder *et al.* 2004), and the future of island biogeography theory in general (Brown & Lomolino 2000). Only two papers cited here refer explicitly to volume-effects on species richness, both concerning coral reef (Chittaro 2002, Belmaker *et al.* 2007). We suggest that sampling habitat volume may be a better predictor of species richness than area-relationships alone. Spatial scaling is an important organizing principle of biogeographical patterns (Whittaker 2000), and it remains to be seen what effect spatial-scale may have on SVR.

Extinction rates have thus far been largely based on a handful of more easily studied yet species-poor groups (birds, mammals and palms) (Balmford *et al.* 2003). Given the rapidly changing nature of the Earth's biosphere, clearly estimates are needed for alterations in currently poorly understood but biodiverse groups such as arthropods. We suggest that further exploration of the ideas proposed here, specifically SVR in complex ecosystems, may prove fruitful.

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