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Community ecology of tropical forest snails: 30 years after Solem

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Abstract

Since Solem's provocative claim in the early 1980s that land snails in tropical forests are neither abundant nor diverse, at least 30 quantitative-ecological papers on tropical land snail communities have appeared. Jointly, these papers have shown that site diversity is, in fact, high in tropical forests; often more than 100 species have been recorded per site, which is somewhat more than normally found at sites in higher latitudes. At the same time, however, point diversities (which usually range between 10 and 30 species per quadrat) appear to be no different from the ones recorded for temperate localities, which suggests that the number of ways in which syntopic resource space can be subdivided among different land snail species has an upper limit that is no higher under tropical conditions. The available data do not allow much analysis of the ecological structuring processes of communities besides very coarse ones, *e.g.* the proportions of carnivores versus herbivores and Pulmonata versus non-pulmonates. Also, these first 30 years of research have shown that a number of serious methodological and conceptual issues need to be resolved for the field to move ahead; in particular whether empty shells from the forest floor may be used as a proxy for the contemporaneous communities. I make a number of suggestions for ways in which these obstacles may be removed. First, studies should be preceded by exploratory nested sampling in contiguous quadrats of increasing size, spanning several orders of magnitude. The shape of the triphasic species-area curve and non-linear regression of the small-area end of the curve will help identify the quadrat and site areas that allow ecologically more meaningful studies. Second, researchers should be more aware of the trophic levels of species and restrict their analyses within guilds and within body size classes as much as possible. Testing species abundance distributions against ecologically explicit theoretical models may be a fruitful avenue for research. Finally, I argue that studies of this nature require species abundances that may only be found in tropical land snail communities that live on calcareous substrate, and therefore I suggest that malacologists aiming to understand community structure focus on limestone sites initially.

Contents

Introduction

Almost all papers on tropical land snail diversity include a reference to Solem's seminal paper of 1984 (Solem, 1984), in which he surmised that land snails in tropical rainforests are 'neither diverse nor abundant'. Solem's statement was based on very little evidence and was mostly conjectured from ecological generalizations about rainforests such as their sparse leaf litter, high incidence of fires, and high predation rates. As such, it was deliberately provocative, aimed at spurring tropical malacologists into action to prove him right or wrong. After all, whereas in the early 1980s studies of tropical rainforest insect diversity were in their heyday (Sutton, 2001), similar studies of Mollusca were still virtually non-existent, and Solem was right in calling attention to this lag. Not only are molluscs on land generally considered the next most-diverse phylum after the Arthropoda (Chapman, 2009), they have four ecological characteristics that allow their students to answer questions about tropical forest ecology that complement those addressed by entomologists. First, whereas the greatest diversity in tropical insects is in the monophagous and oligophagous herbivores, niche differentiation among land snails tends to be related to soil type, soil structure and bedrock type, as well as microclimatic aspects of the habitat. Second, snails' extremely low vagility would result in lower point diversity but greater species turnover than for insects. Third, the fact that almost the entire malacofauna accumulates as empty shells on the forest floor may allow for more exhaustive and unbiased sampling methods than in other groups of invertebrates. And fourth, the presence of a single land snail individual in a site will almost always signify the presence of a population, and rarely represent an incidental migrant, as might be the case in more mobile taxa (Cameron, 1998).

The almost 30 years that have passed since Solem appealed to the malacological community (his 1984 paper was presented to the 8th International Malacological Congress in Budapest, 1983), have seen a steady increase in quantitative ecological studies of forest malacofaunas in tropical Africa, Southeast Asia, and, to a lesser extent, Central and South America. Besides proving Solem wrong, these studies have produced a first spectrum of insights into point diversity, species turnover, community structure, determinants for species abundance distributions, altitudinal and edaphic gradients in species diversity, and have made inroads into using land snails as model systems for biodiversity monitoring and as targets for conservation. In addition, the diversity of sampling methods used has highlighted certain methodological issues. In this paper, I present a synthetic review of the literature (specifically: quantitative studies of more or less complete terrestrial snail and slug communities in tropical forests, inclusive of tree plantations and timber production forests, but excluding mangroves), point out important gaps in our knowledge, and give recommendations for future work. Where relevant, I also refer to the considerably larger body of work done on terrestrial gastropods outside of the tropics. Although I do discuss changes in community structure over short distances (<10 km) and along local elevational and land-use gradients, I will not deal with the longer-distance beta-diversity ('allopatric diversity' *sensu* Solem, 1984).

Sampling methods

Like all descriptive/analytical studies of communities of species, a manner of controlled sampling of these communities is called for. Students of tropical forest snail communities have tended to use a nested sampling design, usually consisting of replicate small units (regardless of their square or circular shape (which may influence sampling - see Brummer *et al*., 1994), they are here termed 'quadrats', after Cameron and Pokryszko, 2005) that together represent a sample of the land snail community within a larger unit or 'site', which, in turn, could be grouped into 'areas' (Cameron and Pokryszko, 2005). Typically, quadrats comprise a more or less homogeneous macrohabitat and have a surface area that ranges from the 8 m^2 that Reuben Clements used to sample limestone outcrops in Peninsular Malaysia (Clements *et al*., 2008; Liew *et al*., 2008) to the 400 m^2 plots introduced by Ken Emberton (Emberton *et al*., 1996; Emberton, 1997) in Madagascar and used since by various other researchers in Africa (De Winter and Gittenberger, 1998; Oke and Alohan, 2006; Oke *et al*., 2008) and Asia (Schilthuizen and Rutjes, 2001; Liew *et al*., 2010). A number of quadrats are arranged throughout a site either randomly (*e.g*. Fontaine *et al*., 2007a) or systematically along transects (Emberton, 1997; Emberton *et al*., 1999; Schilthuizen *et al*., 2002; Clements *et al*., 2008; Raheem *et al*., 2009). Although Cameron and Pokryszko (2005) consider sites to be small (< 1 km^2) I here include in the 'site' category entire forests (*e.g*. Fontaine *et al*. (2007a) used 116 randomly placed quadrats to sample Lopé National Park in Gabon), forest fragments (Sri Lankan forest fragments were sampled with transects of twenty quadrats each by Raheem *et al*. (2009)), or predefined plots within forests, such as the 1 km^2 block in Danum Valley Conservation Area in Borneo that Schilthuizen and Rutjes (2001) sampled with 36 randomly placed quadrats. Areas, finally, could be any grouping of sites to a higher hierarchical level, which is a spatial scale beyond the scope of this paper. Although most studies sample quadrats only once, some workers have maintained quadrats for longer periods for resampling in consecutive seasons (De Winter and Gittenberger, 1998; Bloch *et al*., 2007) or even decades (Vermeulen, 2003; Bloch *et al*., 2007).

Quadrat sampling

Sampling within a quadrat usually takes place by manual search (by day and/or night) of suitable microhabitats, usually standardized by searching effort, expressed as person hours. This is then complemented with either or both of the following bulk methods: beating and shaking of (a standardized number of) branches over an inverted umbrella, and (as advocated by Emberton *et al*., 1996) collecting, sieving and sorting (with or without flotation) a standardized amount of leaf litter and/or soil (either sampled randomly across the quadrat or extracted from predefined blocks—the ‘Oekland sampling’ of Cameron and Pokryszko, 2005). The following are examples of different sampling regimes within quadrats. Bloch *et al.* (2007) looked for live snails and slugs at night for 0.5 person-hour in circular 3-m-radius plots in Puerto Rico, did not disturb the litter, and returned the animals after identification. De Winter and Gittenberger (1998) spent two person-hours searching in 20 × 20 m quadrats in Cameroon; this searching time included beating of the vegetation, 0.5 h searching of tree trunks, and collection of four litres of litter, which was subsequently sieved, dried, and searched manually in the lab. Clements *et al.* (2008), finally, sampled West-Malaysian karst forests by collecting four litres of litter and topsoil from 2 × 4 m quadrats at the bases of limestone cliffs. This was then enriched by coarse sieving, flotation (the collection of flotsam after submergence in a bucket of water), drying, and further sieving in a sieve cascade.

Quadrat size

While some authors have adopted near-identical sampling techniques to improve comparison across studies (*e.g.* De Winter and Gittenberger, 1998; Schilthuizen and Rutjes, 2001; Cameron *et al.*, 2003; De Chavez and De Lara, 2011), others have pointed out that sampling methods are best optimized for completeness under the prevailing conditions (Cameron and Pokryszko, 2005). Liew *et al.* (2008) computed incidence-based completeness estimators (*ICE*; Chao and Lee, 1992; Chazdon *et al.*, 1998) for hexaplets of quadrats in limestone and non-limestone forests across Malaysia and found that the ones from limestone had high (c. 90%) completeness, regardless of quadrat sampling intensity, but the ones away from limestone were significantly incomplete. For most community-ecological purposes, therefore, sampling regimes are best optimized for the expected local species diversity and abundance (since completeness is generally a prerequisite for any kind of analysis), rather than for comparison with other studies.

Having said that, some further consideration of the concept of ‘completeness’ may be warranted. As Cameron and Pokryszko (2005) imply, an inventory of a quadrat is complete if all species actually present are found. However, in species with such limited active dispersal capacities as land snails, species ‘presence’ is an elusive concept. Even in medium and large-bodied (sub)tropical land snails, active dispersal rates are often in the order of just 1-5 m gen^{-2}, leading to extremely narrow demes of tens of metres across or less (Schilthuizen and Lombaerts, 1994; Parmakelis and Mylonas, 2004; Giokas and Mylonas, 2004; Schilthuizen *et al.*, 2005b). In the small-bodied microsnails in complex three-dimensional microhabitats that often dominate tropical snail communities, the scale of well-mixed population units is likely to be much smaller, and substantial heterogeneity may already be present below the scale of standard quadrats. In other words, a 20 × 20 m quadrat may contain 35 species, but only subsets of these may actually be co-existing in the sense that they share the same resources and potentially engage in ecological interactions with one another (the ‘point diversity’ of MacArthur, 1965). It is important to keep in mind that such clumping in land snails is fundamentally different in character from similar patterns of micro-scale clumping in organisms with mobile individuals, gametes, or seeds; in the latter cases, micro-scale clumping of adults affects demographic and genetic population structure much less than in land snails, and some of the unevenness seen in adjacent quadrats along transects (*e.g.* Schilthuizen *et al.*, 2002; Dinarzarde Raheem, unpublished data) may thus be real rather than sampling artefacts. It also means that, in order to decide on the quadrat size adequate for capturing true alpha diversity in a certain habitat (*i.e.*, the remaining diversity after area has been factored out), we may need to do a pilot study on a series of contiguous, nested quadrats, and determine the y-axis intercept q in the fitted Arrhenius equation $S = q + cA^z$ (Rosenzweig, 1995); see Fig. 1. The largest quadrat size that has an S not significantly different from q could be taken as the preferred quadrat size.

Sampling previous generations

Another methodological issue that repeatedly comes up, at least in studies on non-acidic soils, is the inclusion of empty shells in the sample. While some authors have deliberately limited themselves to the contemporary populations by sampling living snails only (*e.g.* Alvarez and Willig, 1993; Bloch *et al.*, 2007), most have included empty shells in their sampling either by necessity (in many tropical forests, live snails and slugs are extremely hard to find) or by design. Clements *et al.* (2008) and Schilthuizen *et al.* (2002), for example, sampled *only* empty shells, and most other studies mix living snails and empty shells. Often, the empty shells form the majority of specimens:

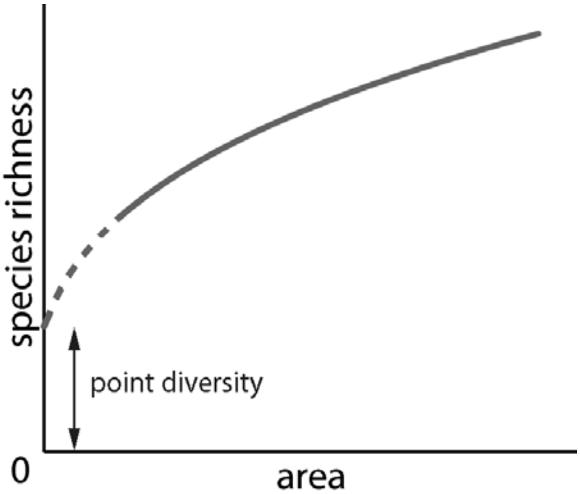

Fig. 1. The y-axis intercepts *q* for the fitted Arrhenius equation $S = q + cA^z$ represents point diversity and may be estimated from a non-linear regression of data at several non-zero area sizes.

the pristine and disturbed Bornean karst forest samples in Schilthuizen *et al.* (2005a), for example, contained less than 1% living animals.

Sampling empty shells has both advantages and disadvantages, depending on the study objectives. Among the advantages, the possibility to sample almost the entire malacofauna in a more or less unbiased fashion stands out (more or less unbiased, because there will be a bias towards the larger, thick-shelled species to survive weathering for much longer); this has proven useful for biogeographical questions addressing species-area relationships (Clements *et al.*, 2008). All shelled snails and semi-slugs, living at all forest strata will eventually end up as empty shells on the forest floor – provided they do not live in enclosed spaces like phytotelmata (Kitching, 2000), nest ferns (Ellwood and Foster, 2004), or social insect nests (Eguchi *et al.*, 2005). Sampling shells from the forest floor is thus comparable in efficiency to insecticide fogging for canopy insects (Coddington *et al.*, 1991). Also, in theory, comparisons of previous diversities with present-day diversities could reveal changes in species composition, provided the empty shells date back long enough and can be dated (see below). In most studies, however, the empty shells are assumed to represent the contemporary malacofauna, which is only correct if the shells are younger than an average snail generation (Cernohorksy *et al.*, 2010). The truth is that we still know very little about the rate by which shells on the forest floor degrade and dissolve. While Solem (1984; on authority of P. Mayhill) states that in New Zealand, 'the rate of shell decay is a fast three weeks during dryer periods and less than ten days when the litter is wet', Cameron and Pokryszko (2005), on the other hand, make the point that in calcareous areas, empty shells may actually be ancient or subfossil. The presence of old specimens in the sample is particularly problematic if sites are compared where major land use changes have taken place. For example, Schilthuizen *et al.* (2005a), Oke *et al.*

Fig. 2. A large number of microsnails from a limestone hill in Kelantan, Malaysia, collected as empty shells. Photo: Reuben Clements.

(2008), and Tattersfield *et al*. (2001b) all included empty shells in their sampling, which was intended to study the impact of logging, quarrying, and forest-to-plantation conversion on the snail communities. These impacts may have been underestimated if their samples included remnants of the pre-disturbance faunas. Similar problems exist with other natural skeletal death assemblages such as vertebrate bones (Terry, 2010a, b).

There are several ways in which these potential problems may be assessed, but few have been explored properly. An indirect method would be to compare the contemporary species diversity with the one apparent in the empty shells. If there are no obvious discrepancies, the samples may be pooled (Rundell and Cowie, 2004; Cameron and Pokryszko, 2005) and safely assumed to represent the present-day populations. Direct measurements of shell degradation are, however, very rare, especially for tropical settings. Lee (2009) reviews several published (*e.g.* Barrientos, 2000; Pearce, 2008); and unpublished experiments which appear to indicate that shell dissolution takes between several months and several years, depending on size and environment, and that it is bioerosion (calcium harvesting by other organisms), not chemical dissolution, that is the main factor responsible for shell disappearance. However, the admirably tenacious multi-species, long-term experiments that Pearce (2008) did in Delaware (and similar experiments are underway in the Czech Republic; Řihová *et al*., 2010) are yet to be replicated in tropical settings. Relatively small soil samples taken from the foot of limestone cliffs can sometimes yield enormous numbers of shells (Fig. 2; see below) and it is hard to imagine that these represent the 'graveyard' of the local fauna for just the most recent years. Intercepting falling shells with trays placed at the foot of the hill or using radiometric or amino-acid racemization dating of shells in the soil (Pigati *et al*., 2004; Hearty and Schellenberg, 2008) might be suitable methods to answer this important question.

Local species richness and diversity

If the past 30 years have shown anything, it is that Solem's (1984) prediction that land snails in tropical forests are species-poor was incorrect. The highest land snail species diversities on record now all come from tropical sites, and no longer from wet-temperate locations (*e.g.* New Zealand's South Island), as was the case when Solem wrote his review. In Borneo, Vermeulen (2003) recorded 108 species in three days' collecting in the 31 km^2 Batu Niah National Park, whereas Liew *et al*. (2010) collected 109 species from 142 quadrats in the 754 km^2 Kinabalu Park. Emberton (1995) reports on 'a small patch of lowland rainforest' adjacent to the village of Manombo in Madagascar where 52 species live sympatrically. Rosenberg and Muratov (2006) found 91 species on a single one-hectare site in Jamaica. Schilthuizen and Rutjes (2001) found 61 species in a 1 km^2 block of lowland rainforest in Borneo. De Winter and Gittenberger (1998), finally, recorded 97 species from a square kilometre of Cameroonian forest. Also in individual quadrats, high species richness has been found. The richest ≤400 m^2 quadrats have yielded 30 species in Western Kenya (Tattersfield *et al*., 2001b), 48 species in West Malaysia (Liew *et al*., 2008; Clements *et al*., 2008), 44 species in Uganda (Wronski and Hausdorf, 2008, 2009), 45 species in Cameroon (De Winter and Gittenberger, 1998), and 42 species in Jamaica (Simpson (1894: 112) reports 'in a narrow limestone gorge of the Rio Cobre near Bogwalk in the talus under a ledge some two rods long we found no less than forty-five species, all living....').

Solem did appear to be correct, though, about the low abundances in tropical forests. The high species numbers from acidic rainforests mostly were painstakingly accumulated from small numbers of individuals from many quadrats, representing a great collecting effort and a relatively meagre output. The 142 Kinabalu quadrats of Liew *et al*. (2010) yielded only 2,832 specimens; the large study in Cameroon by De Winter and Gittenberger (1998) resulted in 2,654 individuals; and a similar collecting effort in Danum Valley (Schilthuizen and Rutjes, 2001) produced just 546 snails. Given that a large portion of the specimens in these studies were empty shells, living populations of tropical land snails may be considered extremely sparse. However, this may just reflect their cryptic mode of life. Many land snails and slugs are nocturnal and are simply not seen during the day. Others are soil-dwelling or canopy-dwelling and also not easily encountered, unless exceptional conditions reveal their true abundance. A few examples from Borneo (Schilthuizen, unpublished) may illustrate this. A single pitfall trap baited with lamb meat and placed in secondary forest gathered (besides the carrion beetles it was intended to catch) almost 400 individuals of *Subulina octona* (Bruguière, 1789), and similar traps in montane forest attracted several dozens of the otherwise rare ariophantid *Kalamantania whiteheadi* (Godwin-Austen, 1891); a heavy rain shower in lowland primary forest washed down many live specimens of *Amphidromus martensi* Boettger, 1894, a tree canopy snail, of which only the empty shells are normally found at ground level.

Still, although true densities may be higher than they appear to be, most tropical rainforests on acidic soil support demonstrably sparser land snail populations than those on alkaline, calcareous soils. Schilthuizen *et al*. (2003a) found that abundances in quadrats on limestone soil in Borneo were up to an order of magnitude higher than in those placed in surrounding non-limestone soils and similar observations were reported for Gabon by Fontaine *et al*. (2007a). Liew *et al*. (2008), in their compilation of a large number of Malaysian limestone and non-limestone plots, showed that the abundances on limestone are on average more than an order of magnitude greater than on other soil types.

It may be worth exploring what was Solem's ecological reasoning for expecting land snails to be species poor in tropical forests. Among the chief factors he invoked were high predation, negligible leaf litter, and frequent fires. However, these ecological rationales may not apply. Among land snails' chief predators, especially in Africa but also in other tropical regions (Schilthuizen *et al*., 2006; Rowson, 2010), are other land snails, which would add to, rather that detract from, land snail diversity. The widely held belief that tropical rainforests have a negligible litter layer is certainly not generally true (see also Corlett, 2009). As pointed out by De Winter and Gittenberger (1998), 'thickness, distribution and composition of litter layers are dynamic in both space and time'. And: 'great diversity in size, shape and firmness of the leaves, combined with differential decomposition rates by spot differences in microclimate, moisture and soil conditions, potentially provides a wide array of microhabitats supporting a high land snail diversity of vegetable and fungi consumers, and associated predator species'. Fire, finally, indeed affects tropical forests periodically, but probably not as disastrously as in many subtropical and temperate vegetations; moreover, since intermediate disturbance can delay competitive exclusion, fire may affect diversity positively rather than negatively (Connell, 1978).

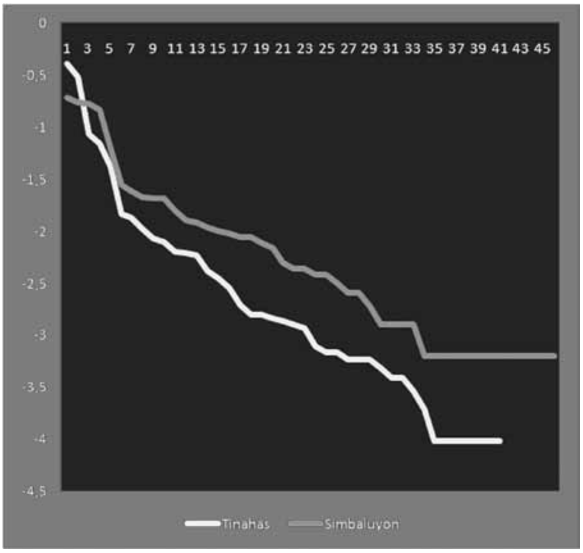

Fig. 3. Species abundance distributions for two samples of limestone microsnail communities in Malaysian Borneo (shell size class 2 - 3.5 mm only). The x-axis shows species rank, from the commonest to the rarest; the y-axis shows log relative abundance.

Species abundance distributions

As soon as their curiosity about the actual species richness of their quadrats, sites, and areas is satisfied, community ecologists working on any taxon tend to turn to the next feature of interest, the species abundance distribution ('SAD'). Tropical land snail researchers are no different: many papers explicitly display the pattern of commonness and rarity among the species found (*e.g.* De Winter and Gittenberger, 1998; Schilthuizen and Rutjes, 2001; Schilthuizen *et al*., 2002, 2005a; Oke and Alohan, 2006). Although this is usually presented as an untransformed bar graph, I will here use the now standard 'Whittaker plots' (Whittaker, 1965; Magurran, 2004; Cameron and Pokryszko, 2005; Nekola *et al*., 2008), which display rank (from commonest on the left to rarest on the right) on the x-axis, and log relative abundance on the y-axis (Fig. 3). SADs are interesting for a variety of reasons. First, they describe the community in a more informative way than by simply enumerating species, as they incorporate heterogeneity in abundance and hence are the basis for calculations of diversity (such as the Simpson Index; Magurran, 2004). Second, the rare-species tail of the SADs allows estimation of the numbers of species missed altogether and, therefore, of the true species richness. Chao (1984) developed a simple, non-parametric estimator for this, based on the numbers of singletons and doubletons in the sample. In many studies, percentages of singletons are high (11%, 12%, and 23%, respectively, in De Winter and Gittenberger, 1998; Fontaine *et al.*, 2007b; Liew *et al.*, 2010), leading to relatively high richness estimations. Third, SADs allow seasonal (De Winter and Gittenberger, 1998) or disturbance-induced (Schilthuizen *et al.*, 2005a) changes in species dominance to be visualized. However, the property of SADs that has most captured the imagination in recent years is the possibility to deduce from them the ecological processes underlying the community structure. For example, George Sugihara (Sugihara, 1980; Sugihara *et al.*, 2003) developed a model for sequential subdivision of niche space which results in SADs that approach the lognormal distribution seen in many natural communities, including those of gastropods. (In a Whittaker plot, a lognormal distribution would give a sigmoid curve that first descends fast, then levels off, then descends again.) However, a distinct right-skew – an overrepresentation of rare species – is often observed (Tokeshi, 1999), and Hubbell (2001) showed that a niche-free 'neutral' model in which slots in the community are filled randomly (the zero-sum multinomial) is better at predicting this skew. Testing goodness of fit between the predictions of particular models and an observed SAD should lead to an insight into the potential ecological processes structuring the community, as Cameron and Pokryszko (2005) did for a few tropical and non-tropical land snail communities (although many SADs available in the literature may suffer from the fact that they have been obtained with sampling methods that are not particularly unbiased; Cameron pers. comm.). However, a caveat is in order as indications exist that the properties of SADs are shared by many highly unrelated patterns both in nature and in culture and may reflect general statistical properties of all complex dynamical systems. If true, then this would limit the possibility to extract the ecological structuring processes from the shape of SADs alone (Nekola and Brown, 2007).

It should be stressed, moreover, that most biological SAD models only apply to a single guild in a single community. 'Single guild' and 'single community' are criteria that, in land snails, require a little elaboration. First, we have, above, already dealt with the concept of a single community, and I argue that this concept applies only at the spatial scale where true point diversity is in effect (a scale possibly smaller than most quadrats). If SADs are determined at a substantially larger spatial scale, the chances of finding patterns that derive from ecological rather than statistical causes decline rapidly (Šizling *et al.*, 2009). Second, a guild is a community of species 'with a similar ecological function' (Rosenzweig, 1995), competing for roughly the same resource (Hubbell, 2001). To consider communities of tropical land snails as guilds would probably be wrong. Even with our stunted knowledge of tropical land snails' autecology, we are certain that, for example, many African faunas are composed to a considerable fraction of predators (De Winter and Gittenberger, 1998; Wronski and Hausdorf, 2008), and even among non-molluscivores, sizeable but unknown proportions of fungivores, folivores, and detritivores could probably be distinguished. Yet another factor to be reckoned with is body size: throughout its life, a snail's body mass passes through several orders of magnitude, and since it is likely that ecological interactions are stronger among individuals of similar size, we should really consider different size classes as different communities. This would imply that the juveniles of a particular species would sit in a different community than the adults. (As an aside, it may even be incorrect to consider such a community to be composed of land snails only, as some snail species may compete with other low-mobility invertebrates - Isopoda, Diplopoda, certain Coleoptera - more strongly than with other snails, as do marine invertebrates in a similar community, the rocky intertidal (Connell, 1961; Wootton, 1994).)

Ecological diversities

Although large, small-scale samples are required to distill structuring processes from SADs, the community structure may also be assessed in a more qualitative manner, by distinguishing functional groups within the malacofauna (Emberton, 1995). Unfortunately, as mentioned above, our knowledge of the niches and trophic levels of tropical forest snails is still extremely limited. Anecdotal information exists on carnivory, necrophagy, fungivory, frugivory, and folivory in some species (see above), but these data are without exception too few and scattered to compare entire communities. Until more detailed data are available, only more coarse patterns in composition can be studied.

One of these is the proportion of 'non-pulmonates' (mostly Caenogastropoda and Cycloneritimorpha). In the Cameroonian fauna sampled by De Winter and Gittenberger (1998), only three out of the 97 species are non-pulmonates (one cyclophorid and two maizaniids), all of moderate rarity. Conversely, Bornean faunas have roughly 50 : 50 proportions of Pulmonata and non-pulmonates (Schilthuizen *et al.*, 2006a), whereas

Raheem *et al.* (2008, 2009) recorded about one-third non-pulmonates in Sri-Lankan faunas. These differences are quite mysterious and may require composite explanations from both evolutionary ecology and historical contingencies. Schilthuizen *et al.* (2005a) showed that in Borneo, where pulmonates and non-pulmonates are roughly equally speciose and abundant, the former dominate in limestone habitats that are pristine, whereas Pulmonata do in ones disturbed by fire and/or logging (Fig. 4). This underscores the observation (Solem, 1974) that non-pulmonates are less resistant to drought and less able to survive under extreme conditions – which may also explain why most, if not all invasive snails are Pulmonata. If the proportion of non-pulmonates would generally be determined by the degree of seasonality, then this may be behind global and regional differences as well. A systematic study of drought-related climate parameters in relation to non-pulmonate species richness and commonness may reveal such patterns.

Another conspicuous large-scale difference among tropical mollusc faunas is the proportion of carnivores. Workers studying the Afrotropical and Madagascan faunas, have repeatedly highlighted the large proportions of the exclusively molluscivorous family Streptaxidae in their samples. In many sites in tropical Africa, about a quarter of the species are streptaxids (Emberton *et al.*, 1997; Tattersfield *et al.*, 2001a; Fontaine *et al.*, 2007b; Wronski and Hausdorf, 2008), and in the study by De Winter and Gittenberger (1998) in Cameroon, this proportion was even as high as 34%. In other faunal regions, the proportion of carnivores (as far as is known) is generally much lower: in most limestone sites in Sabah, only two known carnivore species (one diapherid and one rathouissid) occur among up to 100 non-carnivorous species; Schilthuizen, unpublished data), and in the Manakau Peninsula of New Zealand, only four (Rhytididae) out of 72 species are carnivores (Solem *et al.*, 1981). The causes for these differences are totally unclear. De Winter and Gittenberger (1998) have speculated that the African streptaxids occupy niches filled by non-Mollusca in rainforests in other tropical regions, but even within East Africa (especially along elevational gradients) and in Southeast Asia (regionally) strong differences exist in the proportions of the carnivorous Streptaxidae and Diapheridae, respectively (Tattersfield, 1996; Emberton *et al.*, 1997; Tattersfield *et al.*, 2001a; Clements *et al.*, 2008). Stable-isotope studies (Michener and Lajtha, 2007) in combination with considerations based on evolutionary rates of ecological traits and historical biogeography may be required to understand better the trophic levels occupied by members of different tropical snail communities.

In the absence of detailed information on niches and trophic levels of the constituent species, morphospace patterns may serve as a proxy. It is well-known that land snail size and shape are adapted to abiotic and, to some extent, also to biotic aspects of their niche and habitat (Cain, 1977; Goodfriend, 1986). In principle, thus, differences in community structure should to some degree be reflected in differences in morphospace occupied. Several studies (*e.g.* Peake, 1968; Emberton, 1995; De Winter and Gittenberger, 1998; Liew *et al.*, 2010) have looked at this. Part of

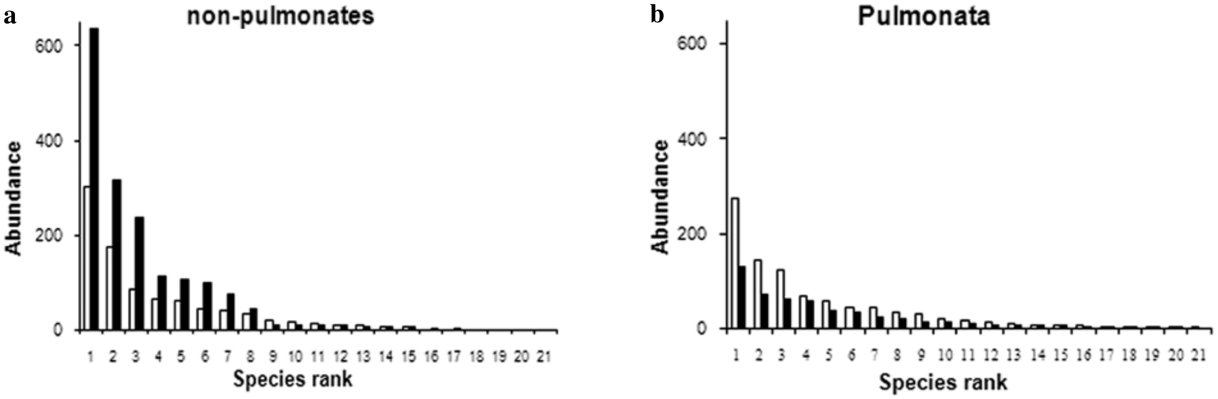

Fig. 4. Species abundance distributions for a Bornean limestone hill (Mawas). Non-pulmonates (a) and Pulmonata (b) are shown separately, as are the patterns for disturbed (open bars) and pristine (filled bars) quadrats. The patterns show that in disturbed habitats, Pulmonata increase in dominance at the expense of non-pulmonates (after Schilthuizen *et al.*, 2005a).

these treatments consider patterns in shell size or shell diameter, which I shall not discuss here because these will be related to species-biomass distributions and thus largely a different manifestation of the same dynamic ecological processes that generate the SAD (Henderson and Magurran, 2010). As for patterns in shape, several ways of distinguishing shape categories have been developed. The most applied is Cain's (1977) shell height/width index, which in many faunas has a bimodal frequency distribution and tropical faunas seem to be no exception (Fontaine *et al.*, 2007b), although the presumed relationship of these modes with vertical and horizontal substrates is not confirmed (Emberton, 1995; De Winter and Gittenberger, 1998). Emberton (1995) performed an admirable analysis on snail assemblies from North America, New Zealand, and Madagascar, in which he used forest structure data to predict the shell shape proportions from the available 'flat', 'globose', and 'tall' spaces in the habitat and combined these with phylogenetic constraints in shell shape within the dominant families. For the Madagascan fauna, this approach suggested that phylogenetic constraints were more important for structuring the morphospace than ecological niches. Yet, Emberton advocates developing more information-rich methods for evaluating morphospace, *e.g.* by applying Raupian coiling parameters rather than height/width measurements. In an attempt to enlarge the set of data used for assessing morphospace, Liew *et al.* (2010) added aperture height and width to shell height and width and reduced these four parameters to two principal components to show that occupied morphospace (and presumably also niche space) declined with increasing elevation, which they attribute to the reduced primary productivity. Further basic studies exploring the potential for morphospace to reflect more or less accurately the underlying ecological diversity are certainly needed, and measures such as the disparity index developed by McClain (2005) for deep sea gastropods may be useful.

Species diversity gradients and turnover

Although I do not discuss diversity patterns such as 'allopatric diversity' as defined by Solem (1984), which take place at the large scales that arguably fall outside of the realm of community ecology, I will here briefly discuss diversity patterns on the medium spatial scale, that is, within single sites. Such diversity patterns fall into two main categories: those taking place along gradients (*e.g.* elevational, land-use, or humidity gradients), and those represented by quadrat-to-quadrat spatial species turnover. The latter type is the hardest to interpret, and several authors have attempted to distinguish sampling error from 'real' species turnover. Cameron and Pokryszko (2005) have pointed out that frequently used indices for unevenness, such as Whittaker's *I* (the total number of species divided by the mean number of species per quadrat), are prone to sampling error, as they tend to be negatively correlated with sample size: the smaller the quadrat samples (and in tropical land snail studies they often *are* small), the higher the apparent degree of between-quadrat variation. However, as we have above argued that many tropical forest snail populations will be very small and highly scattered, it is unlikely that each quadrat contains demes of all the species present in the site. Therefore, some degree of spatial species turnover is expected, even on small spatial scales. Fontaine *et al.* (2007a,b), for example, in Lopé National Park, Gabon, sampled 116 quadrats differing strongly in forest type, habitat, and degree of anthropogenic disturbance, and found great unevenness; in fact, 22 of the 71 recorded species were found only at single stations. Schilthuizen *et al.* (2002) showed that Whittaker's *I* within 20 × 200 m sites in Sabah was twice as great for non-pulmonates as for Pulmonata, which might at least in part reflect a greater degree of species clustering in the former taxon, possibly related to its narrower ecological tolerances (see above).

In sites where quadrat completeness is high (*e.g.* in limestone areas) and/or where the number of quadrats is very high, and where ecological parameters are measured for each quadrat, multivariate analyses of species-by-ecology may allow sampling error to be distinguished from the habitat diversity responsible for some of the spatial species turnover, although the truly relevant parameters may often be missed. However, if the changes take place along obvious gradients in one or several parameters, it is easier to distinguish sampling from ecological effects. Alvarez and Willig (1993) sampled across treefall-gaps in Puerto-Rican forest and recorded the appearance, disappearance and indifference of macrosnail species with regards to the gap habitat. Liew *et al.* (2010) and Tattersfield *et al.* (2001) sampled long elevational transects on Mount Kinabalu and Mount Kenya, respectively, and were able to map the community change over elevational gradients (Fig. 5).

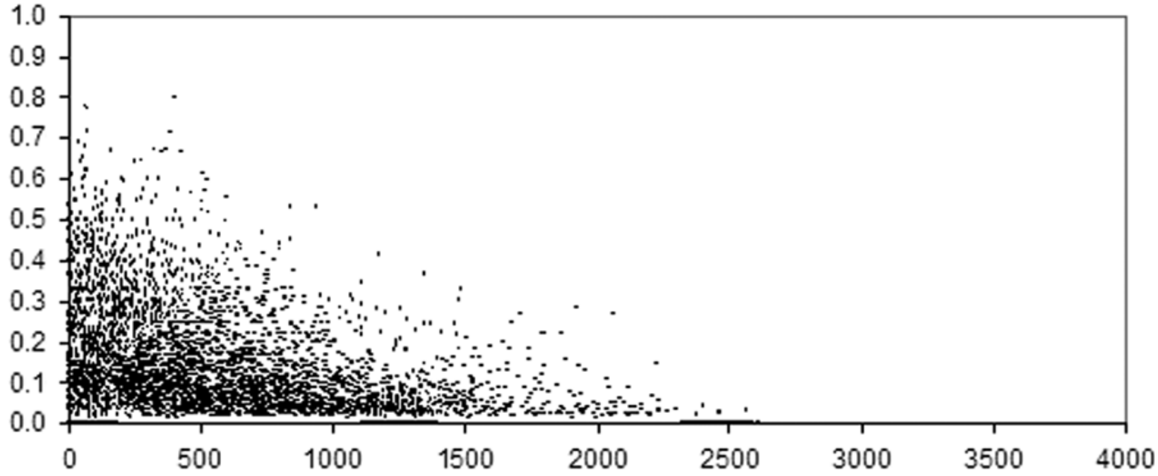

Fig. 5. Pairwise community similarities among 142 quadrats taken along elevational transects on Mount Kinabalu, Borneo. The x-axis shows Jaccard's index for pairs of plots; the y-axis shows the corresponding difference in elevation for each pair (this figure is based on the work published in Liew *et al.* (2010); the diagram itself has not been published before).

Conclusion and outlook

The latitudinal gradient in species richness is probably the single most obvious macro-ecological pattern, with species richness on both hemispheres declining with increasing latitude; this pattern is seen in the vast majority of taxa (Brown and Maurer, 1989; Rosenzweig, 1995; Gaston, 2000). In land snails, however, the trend is less than obvious. Although recorded quadrat richness in tropical localities can sometimes be as high as 48 species, and is thereby higher than previously expected (Solem, 1984), this is, in fact, not substantially greater than quadrat richness in subtropical (Stanisic *et al.*, 2007; Cameron *et al.*, 2003) and temperate (Cameron and Pokryszko, 2004; Nekola and Smith, 1999) localities. At a larger spatial scale, tropical land snail species richness is more conspicuously higher than those at higher latitudes due to greater rates of faunal turnover (Nekola, 2005; Stanisic *et al.*, 2007). However, the limited degree of elevated point diversity in the tropics and the much smaller scale at which the first phase transition occurs in Rosenzweig's (1995) triphasic species-area curve are perhaps the more interesting phenomena, because in these respects snails differ most from other taxa (notably insects (Morse *et al.*, 1988) and plants). The fact that tropical forest snail communities appear to reach almost the same maximum point diversity as temperate ones may suggest that the number of ways in which resource space can be subdivided is quickly exhausted and probably not directly related to the surrounding biotic diversity, but more likely has to do with the available microclimatic and microchemical gradients.

For this reason, perhaps, now that land snail point diversity in the tropics appears to be higher than expected, our next challenge is understanding why it is not *even* higher. For this, a new style of study will be required. First, more than has been the case until now, malacologists will need to 'think like a snail'. That is, design their sampling and experiments in such a way that they take place at the scale relevant for the questions to be answered. In many ways, our methods are still burdened by the fact that they have been adopted from methods developed for other organisms, with diversity patterns at scales many orders of magnitude greater. Hence, studies should be preceded by an exploratory nested sampling at ever increasing spatial scales to map the shape of the species-area relationship. Although limited in the largest scales by the fact that complete surveying is needed, this allows an estimation of the appropriate quadrat size. A second exploratory sampling at that quadrat size may then permit an assessment of the correct sampling effort to reach acceptable completeness and abundance for species-abundance distributions. Finally, samples should be segregated into classes of equal body size and separate guilds.

Such a series of conditions, however, poses practical constrictions: low abundances will usually prevent

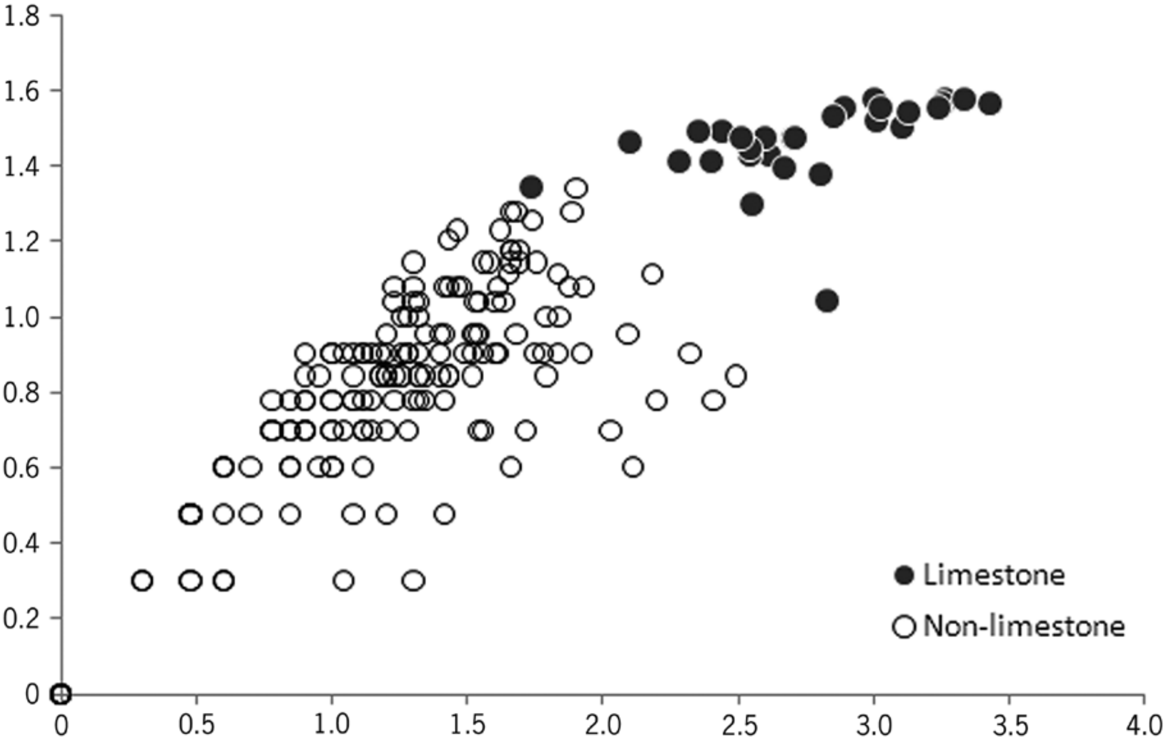

Fig. 6. Richness vs. abundance log-log plot for quadrats sampled in forest on limestone (closed symbols) and away from limestone (open symbols), showing that perceived species richness of limestone habitats is an illusion created by higher abundances (modified after Liew *et al*., 2008).

a single size class for a single trophic level in a quadrat of just a few square m to be sampled with any acceptable degree of completeness. An exception, however, are the communities of microsnails that feed on the microvegetated surfaces of limestone rocks (Clements *et al*., 2006). In these communities, population densities are generally very high, *e.g.* using 25 × 25 cm census quadrats, Berry (1961) and Schilthuizen *et al*. (2003b) measured average adult densities of 129-724 per m^2 for *Opisthostoma* species in Malaysia. Another advantage of sampling such limestone rock faces (provided that the potential problem of time-averaging of death assemblages is resolved; see above) is that a steady accumulation of dead representatives collects at the foot of a vertical limestone wall, amounting to thousands of individuals, which can be obtained and separated into size classes by flotation and sieving with differing mesh sizes. Finally, Schilthuizen (2000), Schilthuizen *et al*. (2003a), and Liew *et al*. (2008) showed that besides their higher abundances, limestone communities are not particularly exceptional: their apparently higher richness is an illusion caused by the higher abundances (Fig. 6). Also, very few species are obligate limestone-dwelling: the vast majority are also found in adjacent non-calcareous habitats. Similar results were obtained by Nekola (2011) for temperate snail faunas.

As an example of the potential of studying SADs in these communities, I sampled quantities of c. 10 i of litter and top soil from underneath flat, near-vertical microvegetated limestone rock faces of 5 × 10 m on several limestone outcrops in Sabah, Malaysian Borneo, and collected the shells by flotation, drying, and sieving. Preliminary data on two such quadrats, ‘Simbaluyon’ and ‘Tinahas’, taken from separate limestone hills c. 10 km apart show that for just one size category (2.0 - 3.5 mm shell diameter), the former yielded 1,590 individuals and 46 species, and the latter gave 10,301 individuals and 41 species (Fig. 7). The large sizes of these small-scale samples are more than sufficient to test SAD models within ‘true’ communities (Fig. 3). Pooling of SADs from different

Fig. 7. A portion of a representative collection of same-size microsnails from a Bornean limestone hill, showing the numbers achieved for evaluating the species-abundance distribution.

size classes or adjoining quadrats would then allow to test at what spatial scale or body-size scale these models break down to give, *e.g.* canonical lognormal patterns. I would like to encourage students of tropical forest snail communities to focus on such high-density localities and study SADs in nested series of samples, nested in terms of sampling quadrats, size classes, and, ideally, also trophic levels. Only under such ideal conditions can many of the issues raised in this paper be properly addressed, allowing tropical forest snail community ecology to move from the current, descriptive stage into a higher level of analysis and understanding.

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