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REPLY

Taxon-and-Area Invariances, Maximum Entropy, and the Species-Area Relationship

(A Reply to Harte et al.)

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Harte et al. (2009, 2013) argue that maximum entropy theory for ecology (METE) predicts a universal shape of species-area relationship (SAR), which is independent of the focal taxon. More specifically, they claim that the relationship between the local SAR slope z in logarithmic space and the ratio N/S (N for the total number of individuals and S for the number of species; hereafter z - D relationship, where $D = \ln(N/S)$) is universal. Harte et al. (2013) argue that a “biologically meaningful” splitting of the focal taxon just increases the amount of information available, which consequently leads to a more accurate prediction, which is understandably different from a less accurate prediction. They state that such splitting does not violate the universality that was challenged by Šizling et al. (2011). Although we agree that the METE is mathematically consistent, assuming that the constraints used for calculating the most likely state are appropriate (namely, eq. [1c] in Harte et al. 2008, which provides the only biologically relevant constraints; the other constraints are mathematical necessities), we feel that Harte et al. (2013) miss our (Šizling et al. 2011) point. While METE focuses on the most likely prediction of a single observation—which may be the same regardless of which group of species is used—our reasoning concerns possible patterns observed in data.

To understand how it is possible that we can make an universal expectation (like the METE prediction) that can-

not be simultaneously realized in its component subsets, consider the following example. Let us imagine that two boys have realized that their mother had bought one red toy car. Clearly, each of them can equally (universally) expect that he will be given the car. The information is symmetric with respect to them, and with no additional information, their expectation is necessarily the same. However, the situation that both the expectations are simultaneously realized cannot occur, as there is only one toy car in their mother’s handbag. Similarly, in terms of the observed patterns (in contrast to the expectation based on given information), the METE prediction cannot be strictly universal, as it cannot simultaneously hold for a taxon and all its subtaxa (Šizling et al. 2011). We thus disagree with the statements that the data will follow a universal pattern, such as “If, for any choice of a taxonomic group, data on species richness ... are collected and the log-log SAR slopes plotted at each scale against the corresponding N/S values, then ... the graphs will collapse onto ... [a] universal curve in which z is a unique, decreasing, function of ... N/S ” (Harte et al. 2013). Similarly, Haegeman and Etienne (2010) have demonstrated that the METE predictions concerning spatial abundance distribution (which is the basis for the SAR prediction, according to Harte et al. 2008, 2009) are not consistent across spatial scales: the METE prediction at one scale does not necessarily lead to the same configuration as that predicted on a different scale (grain). In fact, the variation of macroecological patterns with taxonomic (focal group) delimitation is tightly related to variation with the scale (area) at which we observe the pattern, as every change of area leads to a change in taxonomic composition (Šizling et al. 2009; Kůrka et al. 2010).

Harte et al. (2009) state that METE predictions have been successfully tested on multiple data sets. There are, however, multiple other theories that have also passed sev-

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eral such data tests, and we thus need a reliable criterion to identify which of the models captures ecological patterns and processes best. A good theory should ideally be able to predict patterns in unknown regions (e.g., estimate diversity at larger spatial scales than those known), infer observed patterns on the basis of incomplete data (e.g., using fossil data), or predict future changes of the patterns. The application of the METE in this respect is relatively limited. For instance, Harte et al. (2013) show that increasing the amount of prior information available leads to a shift in the z - D relationship, obtaining systematically higher values for the predicted slope z . This would suggest that the slope of the SAR is systematically underestimated when based on anything less than complete information. Closer inspection of the data presented in Harte et al. (2009, fig. 1) reveals that many data points deviate by 30%–50% from the predicted value of z . Since the up-scaling procedure is iterative (species richness is calculated for each doubling of area, and using this value again and again for twice-as-large areas in each step), this deviation will accumulate, leading to considerable bias in species richness estimation at scales that are substantially larger than the known (anchor) area. This bias will be even stronger if the number of species and/or individuals in the “anchor” area is estimated with some error, which is virtually always the case (see Royle et al. 2012). Moreover, while the METE predicts a strictly decreasing z - D relationship, leading to a concave log-transformed SAR (decelerating with increasing scale), observed SARs are upward-accelerating at large continental scales (Storch et al. 2012).

The second point of disagreement concerns the proper meaning of the taxon-and-area invariant principle. Although the principle can be used to derive taxon-invariant patterns, it is not its primary aim. Harte et al. (2013) state that “Taxon invariance asserts that the functions describing the macroecological metrics ... should not depend upon the taxonomic choices used to define the assemblage.” However, the principle of taxon-and-area invariance is not a theory that would claim that the patterns should be necessarily invariant against the changes in taxonomic resolution and/or area. It is rather a criterion to evaluate the universality of various theories and an indicator of the potential existence of a fundamental taxonomical and/or spatial level. Macroecological patterns may not be taxon-and-area invariant (and indeed, they often are not)—but in such a case, it makes sense to look for some fundamental level for which the predictions hold and that rule the patterns observed at the other levels (Storch and Šizling 2008). Šizling et al. (2011) have shown that the taxon-invariant relationship between z and D would be unrealistic (different from the observed patterns), which implies that

different delimitations of focal groups of species will often be characterized by different z - D relationships.

Harte et al. (2013) further argue that if we split a taxon into two overlapping groups (i.e., groups which share some species), then the analyst that predicts the SAR on the basis of the whole taxon may obtain the same result as the analyst that predicts the SAR on the basis of the two subgroups (via predicting the SAR for both overlapping subgroups separately, and then summing the two SARs together). They correctly point out that the principle of taxon-and-area invariance therefore cannot be applied on two overlapping groups and the combined species lists. We agree. However, the issue of taxon-and-area invariance arises so long as species can be sorted into nonoverlapping groups, as occurs in any taxonomy or phylogeny, for example, the division of a class into its component orders, or a family into its component genera; indeed, the principle can be applied to any splitting in which different subgroups do not share any species.

Finally, we agree with Harte et al. (2013) that we are left with the puzzle of how to determine the best taxonomic and spatial levels (see also Haegeman and Etienne 2010) to use to generate the most accurate predictions or, in other words, at which fundamental levels the ecological processes work. This is an interesting and open issue for future research but one that arises only once the prospect of a universal (taxon-and-scale invariant) pattern has been abandoned. No one doubts that the predictions presented by METE are much more appropriate null expectations than those based on less sophisticated null approaches, such as models based on random placement of individuals (e.g., Coleman 1981; Williams 1995). However, any prediction based on the principle of maximum entropy is crucially dependent on the set of constraints imposed upon the patterns (Haegeman and Loreau 2008; Haegeman and Etienne 2010; Banavar et al. 2010), and as in all other theories, its validity depends on the validity of its assumption—and it is applicable only within limits given by these assumptions. We feel it is useful to explore these assumptions and limits, as well as the variation around the “most likely expected” prediction, to reveal true scope and usefulness of the theory.

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