Title

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update

Species–area curves and the estimation of extinction rates

The species–area relationship (SAR) is one of the longest-known, most intuitive and empirically best-proven patterns of biodiversity (Arrhenius 1921). Various authors determined theoretically that the SAR can be approximated as a power-law function (i.e., $S = cA^z$ where S is species richness, A is area and c and z are constants; Preston 1962, May 1975, Harte et al. 1999), with $z \approx 0.25$ in continental areas but higher when dispersal barriers are involved (e.g., 'island species–area relationship'). Empirical data suggested lower z in continental areas (0.13-0.18) and values up to 0.35 for island systems (Rosenzweig 1995). Dengler (2009) recently came to the conclusion that the power law fits empirical data best in most cases (see also Dengler & Odeland 2010). Various authors observed further systematic variations of z, such as when considering spatial scale or sampling design (Plotkin et al. 2001, Scheiner 2006, Tjørve 2006, Dengler 2009). Kinzig & Harte (2000) pointed out the difference between SAR and the *endemics–area curve* (EAR), which considers only species endemic to a part of the region under analysis. So what could He & Hubbell (2011) report that was so novel and generally relevant about SARs to merit recent publication in *Nature*?

Since area seems always to affect biodiversity, no matter what taxon, system or scale, SARs have frequently been used to estimate species richness loss resulting from anthropogenic habitat destruction, i.e. extinction rates in a conservation context. The loss of a certain amount of area leads to fewer species existing in a region – at least some regional extinctions occur – and the shape of the SAR has typically been used to retrieve quantitative estimates of how many species will go (regionally) extinct.

Providing empirical evidence for the extinction of a species is challenging and estimating extinction rates across a community even more so (Ladle et al. 2011, this issue). Yet this is needed for many conservation applications, such as schemes for offsetting biodiversity loss (Curran et al. 2011) or, not least, for political argument. It is therefore not surprising that SAR-based estimates of extinction have been welcome despite critical studies that often found lower extinction rates than predicted (e.g., Kinzig & Harte 2000). It was argued, reasonably, that on top of imminent extinction in some species, others will be doomed to future extinction because of reductions in their population size, and that this 'extinction debt' explains apparent misfits. Other sources of uncertainty of the SAR-based estimates are the (often false) assumption of a completely inhospitable matrix between remaining habitat patches (Koh & Ghazoul 2010) or the use of default slope values (z) in the absence of system-specific fitted data.

He & Hubbell (2011) pointed out that a backward interpolation of SARs is a flawed concept of measuring extinction rates (see also Kinzig & Harte 2000). This is because the area gain needed to encounter the first individual of a new species (which shapes the SAR) is always smaller than the area loss needed to remove the last individual. To show this, they formulated both as spatially explicit sampling processes (SAR for first encounters, EAR for last encounters). They concluded that SAR-derived estimates of imminent extinction will always be too high, unless individuals are randomly distributed (i.e., no aggregated occurrence of individuals within a species), which is an unrealistic assumption. He & Hubbell (2011) also showed that the EAR is a good predictor of empirical extinction rates even if no spatial aggregation is modelled, which offers an alternative (but a more challenging one) for estimating immediate extinction of endemics from area loss.

He & Hubbell (2011) clearly acknowledged that there is an anthropogenic extinction crisis and that habitat loss causes extinction. Furthermore, they did not claim that small population sizes of remaining species could not lead to further, lagged extinction (in He & Hubbell's view, EARs model only imminent extinction – and so do SARs, but wrongly). Despite this, He & Hubbell (2011) already anticipated that pointing out this error in estimating extinctions would not be

greeted with enthusiasm among conservationists, and the correspondence on the paper (Evans et al. 2011, Brooks 2011; see also online comments at http://www.nature.com/nature/journal/v474/n7351/full/474284b.html) seems to confirm that. The paper is viewed as irresponsibly undermining conservation efforts by allowing anti-conservation groups to claim that things are not as bad as previously asserted (fossil fuel lobbying in the climate change discussion is cited as example of this tactic). Conserving nature is not only about science, but it is to a large degree politics – and correcting an error leads to better science but might weaken political success. I think scientists must correct themselves and not hold on to preconceived ideas, even if it creates such dilemmas.

However, He & Hubbell (2011) studied area effects as a sampling problem in continental regions, which is probably appropriate for capturing immediate extinction in many conservation settings which occur at the regional or landscape scale. It remains to be understood and tested whether their conclusions – that (a) EAR estimates extinction better than SAR (cf. Kinzig & Harte 2000, Pereira et al. 2012) and (b) z differs systematically between SAR and EAR (which is presented confusingly) – are generalities. Thus it remains to be seen whether SARs *always* overestimate extinction, as He and Hubbell (2011) claimed. A further task will be to quantitatively estimate how many more species may go extinct after a time lag: how large the extinction debt really is (see also Pereira et al., in press). In this context, it may be worthwhile to thoroughly investigate under which circumstances, if any, the consequences of area lost to habitat destruction could be understood solely on the basis of island biogeographic mechanisms (Rosenzweig 2001) – that is, species richness as equilibrium between immigration + speciation and extinction. The spatial and temporal scales of analysis, among other factors, may be relevant for this. Under such circumstances, SARs may estimate the new equilibrium state, accounting for imminent and time-lagged extinctions.

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update

Extinct or extant? Woodpeckers and rhinoceros

Biogeographical research needs accurate data on the distribution of species. For many species this is exceedingly difficult to obtain, leading to a lack of global information collectively known as the Wallacean shortfall. Fortunately, new tools are being developed that allow conservationists and biogeographers to determine the existence of extant populations with much greater accuracy.

Foremost among these new tools is the increasing use of genetic analysis. This was recently used to great effect to confirm the extinction of the Javan rhinoceros (*Rhinoceros sondaicus annamiticus*) in Cat Tien National Park in Vietnam (Brook et al. 2011). Despite their enormous size, Javan rhinoceros are remarkably shy forest-dwelling animals that are difficult to see under natural conditions and were only rediscovered in mainland Asia in 1988. Given the difficulty of traditional surveying techniques, scientists from WWF and the Cat Tien National park had been monitoring the population by conducting genetic analysis of dung samples collected in the park between 2009 and 2010. The analysis indicated that all the dung belonged to a single individual, the body of which was found April 2010, thereby confirming the extinction of the population.

Of course, genetic analysis is costly, time consuming and requires some form of biological tissue (hair, dung, etc.). For many rare animals the only information that exists is the occasional sighting, the reliability of which is often highly questionable. Andrew Solow and his colleagues have recently come up with an ingenious method to account for this inevitable uncertainty (Solow et al. 2011). They use Bayesian (probability-based) statistics to model changes in the rate of valid sightings and to assess the quality of uncertain sightings for the ivory-billed woodpecker (*Campephilus principalis*) in North America. The woodpecker was controversially rediscovered in 2005, but a lack of clear documentary evidence and the failure of subsequent intensive surveys have led many scientists to doubt the veracity of this claim. The Bayesian model applied by Solow to 68 historical sightings (29 of which were classified as uncertain) strongly suggests that the bird is indeed extinct, and the 2005 sighting was sadly a case of mistaken identity.

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