

Review

Climate change, species–area curves and the extinction crisis

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An article published in the journal *Nature* in January 2004—in which an international team of biologists predicted that climate change would, by 2050, doom 15–37% of the earth’s species to extinction—attracted unprecedented, worldwide media attention. The predictions conflict with the conventional wisdom that habitat change and modification are the most important causes of current and future extinctions. The new extinction projections come from applying a well-known ecological pattern, the species–area relationship (SAR), to data on the current distributions and climatic requirements of 1103 species. Here, I examine the scientific basis to the claims made in the *Nature* article. I first highlight the potential and pitfalls of using the SAR to predict extinctions in general. I then consider the additional complications that arise when applying SAR methods specifically to climate change. I assess the extent to which these issues call into question predictions of extinctions from climate change relative to other human impacts, and highlight a danger that conservation resources will be directed away from attempts to slow and mitigate the continuing effects of habitat destruction and degradation, particularly in the tropics. I suggest that the most useful contributions of ecologists over the coming decades will be in partitioning likely extinctions among interacting causes and identifying the practical means to slow the rate of species loss.

Keywords: extinction; global warming; climate change; species–area relationships; biodiversity; prediction

1. INTRODUCTION

Predicting how many species will go extinct as a consequence of human actions is more than just an academic exercise. The potential ethical, practical and economic consequences of widespread species extinctions, leading to reduced overall biodiversity and homogenization of the earth’s biota, have been reviewed widely elsewhere (e.g. Wilson 1992; Kunin & Lawton 1996; Chapin *et al.* 2000; Sala *et al.* 2000; Tilman 2000), and depend to a large extent on the speed and scale of species loss. We need to know how rapidly we are losing species, and, in particular, the relative importance of different anthropogenic factors in causing extinctions. If the main causes of extinctions can be identified, the efforts and resources of conservation organizations can be targeted most appropriately.

Until recently, most conservationists agreed that the major causes of recent, current and future species extinctions were habitat loss and fragmentation, the introduction of alien and invasive species, and over-exploitation (Pimm *et al.* 2001). In combination, these factors are popularly thought to be causing an extinction crisis to rival the mass extinctions seen in the earth’s fossil record. Of these impacts, habitat loss, degradation and fragmentation has consistently been rated as the most important factor causing extinctions. Thus, much of the activity

of conservationists is aimed at reducing the extent of habitat loss, for example by designating reserves or parks, and minimizing its impact, for example by managing habitats in ways that maximize the persistence of populations.

Recently, the conventional wisdom on the major causes of extinction has been challenged. In an article published in the journal *Nature* in January 2004 an international team of biologists predicted that climate change by 2050 would, even in the absence of other threats, doom 15–37% of species to eventual extinction (Thomas *et al.* 2004a; hereafter ‘Thomas *et al.*’). The predicted scale of climate-induced extinctions exceeds even the gloomiest predictions by conservationists concerned about habitat destruction; indeed the authors predict that extinctions from ‘conventional’ threats will be fewer than those caused by climate change. This new research forces us to rethink conservation priorities: to minimize extinctions, should we really focus on reducing and mitigating the effects of climate change, rather than land-use change? If the predictions of Thomas *et al.* are correct, then a dramatic change in the allocation of global conservation resources might be appropriate. Thomas *et al.* argue that further measures to reduce the magnitude of anthropogenic climate change are now the major priority for conservationists.

It is rare for a scientific paper to be the lead item on the evening news, or to fill the front pages of our national newspapers, but the Thomas *et al.* paper

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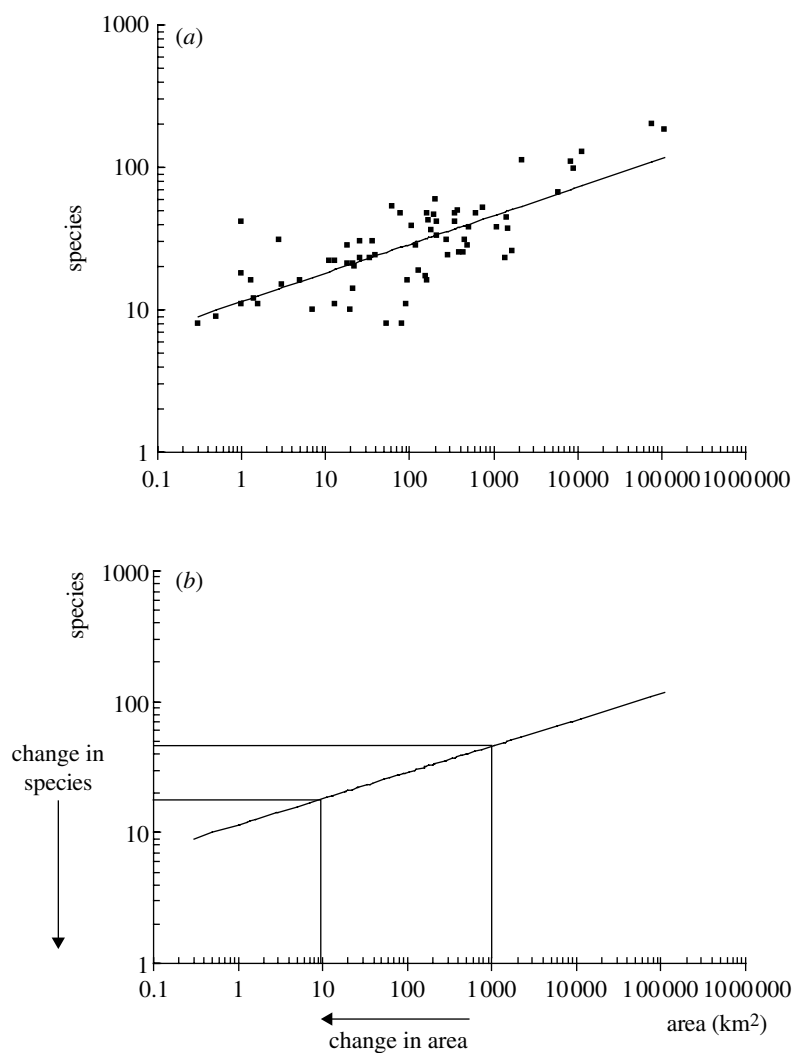


Figure 1. (a) Species–area relationship for butterflies on Caribbean Islands. Note the log-transformed axes. Redrawn from data in Davies & Spencer Smith (1997). (b) Estimating extinctions from habitat loss based on the species–area relationship. For a given reduction in area, the predicted loss of species depends on the slope of the line, z .

received exceptional worldwide media attention. Popular coverage of the Thomas *et al.* paper has been criticized (Hannah & Phillips 2004; Ladle *et al.* 2004). Most scientists would probably agree that the media in a few cases got the ‘wrong end of the stick’, but that the majority of the reporting was reasonably clear and balanced. However, debate about the scientific basis of these and other extinction estimates, as well as their wider interpretation, is important if scientists are to avoid criticisms about ‘crying wolf’ on climate change. Here, rather than dwelling on popular interpretations and misinterpretations of the extinction predictions, I focus on the scientific basis underlying attempts by Thomas *et al.*, and by others, to predict the magnitude of anthropogenic extinctions over the coming century. Many of these estimates, including those by Thomas *et al.*, exploit a well-known ecological pattern, the species–area relationship (SAR). I first discuss the potential and pitfalls of the SAR approach. I then consider the additional complications that arise when applying SAR methods specifically to climate change. I assess the extent to which these criticisms invalidate the predictions of Thomas *et al.*, and attempt to quantify our level of uncertainty over the magnitude and causes of the current ‘extinction crisis’.

2. SPECIES–AREA CURVES AND EXTINCTION PREDICTIONS

The ecological principles underlying many attempts to predict extinctions are straightforward and provide a satisfying (and all too rare) example of the use of ‘pure’ ecology to guide conservation practice. The SAR has been described as ‘ecology’s oldest law’, and in a field where robust generalizations are few and far between, the SAR is perhaps the closest ecologists have to a periodic table. In essence, the SAR describes a widespread relationship between the area investigated and the number of species present. Bigger areas have more species, but the relationship between area and species number is curved: it typically follows a power function of the form $S = cA^z$, where S is the number of species, A is area, and c and z are constants. Thus, on log-transformed axes the relationship between S and A is linear and the slope of the best fitting regression line gives the exponent of the power function, z (figure 1a). Although other forms of curve sometimes describe the empirical data better (Connor & McCoy 1979), the power function is very often the best-fitting relationship between species number and area, and is observed for a diverse range of taxa from bacteria (e.g. Bell *et al.* 2005) to butterflies (e.g. Davies & Spencer Smith 1997).

A straightforward rearrangement of the SAR equation suggests that if we reduce the area of a habitat containing S_{now} species from A_{now} to A_{future} , and assume that z and c remain unchanged, the number of species restricted to that habitat will decrease, eventually, to $S_{\text{future}} = S_{\text{now}}(A_{\text{future}}/A_{\text{now}})^z$ (May *et al.* 1995; May & Stumpf 2000; Pimm & Raven 2000). The form of this calculation is perhaps best illustrated as a figure (figure 1*b*). The key value is z , the slope of the line. The greater the value of z , the greater the loss of species predicted for any given reduction in habitat area. Applications of this approach to predict extinctions have generally taken one of two forms: regional analyses for specific taxa, concentrating on endemics (species confined to the study region; e.g. Pimm & Askins 1995; Brooks *et al.* 1997) and global predictions based on estimates of worldwide habitat destruction (Wilson 1992; May *et al.* 1995). Brooks *et al.* (1997) provide an example of the first approach. Using data on the extent of deforestation on individual islands in south-east Asia they predicted what proportion of birds endemic to each island are likely to be committed to extinction. On a global scale, authors have assumed a biome-wide or global extent of habitat loss, and used this value in the SAR calculation. For example, May *et al.* (1995) calculate that, assuming a z value of 0.25, a 2% loss of rainforest area per year will commit 0.5% of all rainforest species to extinction annually.

Two seemingly picky caveats are nonetheless important in interpreting and discussing the results of such calculations, and have been the root of much of the media misinterpretation of the climate-related extinctions predicted by Thomas *et al.* First, when making global predictions we cannot reliably calculate the number of species likely to go extinct, because the total number of species on earth remains unknown: credible estimates vary by a factor of 10. The best we can do is estimate what fraction of existing diversity will be committed to extinction under different habitat loss scenarios. Second, note the use of the phrase 'committed to extinction'. Species extinctions will not all occur instantly following habitat loss; rather there will be a delay before some new equilibrium species richness value is reached, with species persisting as the 'living dead' for many generations, even when the habitat available to them is insufficient for their long term survival (Diamond 1972; Janzen 1986). The difference between species richness immediately following habitat loss and species richness once a new equilibrium has been reached is known as the extinction debt, and the process by which species richness approaches its new equilibrium following habitat area reduction is known as relaxation (Diamond 1972). No current theory adequately allows us to predict how long this will take (Simberloff 1992), although empirically derived estimates are now available for a few species (Ferraz *et al.* 2003).

Putting these largely semantic issues aside, the deceptive simplicity of the SAR method of estimating extinctions conceals a number of assumptions and complications which are not always made explicit. First of all, there is no *a priori* reason why reducing habitat area should necessarily cause a decline in species richness that tracks the species–area curve: removing

area over an ecological timescale of generations is not a direct reversal of the processes which have added species over evolutionary time (Lomolino 2001). Although the SAR is a robust and general pattern, our understanding of what causes it and what influences its shape is still incomplete (Rosenzweig 1995; Lomolino 2001). If we knew which mechanism or mechanisms were generating the pattern, our estimates of extinction probabilities using the SAR method, and our resulting conservation recommendations, could potentially be made more accurate. The most likely explanations are 'area *per se*' and 'habitat diversity' (Connor & McCoy 2000). The 'area *per se*' hypothesis states that small areas of habitat can support small populations of a given species, and smaller populations are more prone to extinction. Thus, as the area increases the number of species that will be able to maintain viable populations will also increase. This is one half of the mechanism—that dealing with extinctions—proposed by McArthur & Wilson (1967) in their equilibrium theory of island biogeography, which seeks to explain the number of species on islands as a balance between rates of extinction and colonization. The 'habitat diversity' hypothesis suggests that larger areas have a greater variety of habitats, increasing the number of niches available for individual species, and allowing species that require multiple habitats to occur. The empirical data from SAR curves do not allow us to distinguish between these (and other) explanations, without additional information (Connor & McCoy 2000). Nonetheless, even if we cannot be sure of its underlying cause, if the empirical relationship is a strong one then it may still be legitimate to use the relationship to make predictions.

A further set of uncertainties involves the choice of appropriate values of A , z and c to use in the calculations. The extent of future habitat loss ($A_{\text{now}} - A_{\text{future}}$) must itself be predicted, which will rarely be straightforward. Extinction predictions are highly sensitive to the value of z used, but determining the appropriate value of z is problematic. Values of z for real islands, or isolated blocks of habitat that mimic true islands, are typically around 0.2–0.3; z values for 'mainland' areas are lower, indicating a more gradual accumulation of species as area is increased (Rosenzweig 1995). In fact, most applications of the SAR method of estimating extinctions assume a z value (typically in the 'island' range 0.2–0.3), rather than attempting to obtain empirically the appropriate z value for the system under study (cf. Brook *et al.* 2003). The role of the intercept c has been almost entirely overlooked in applications of the SAR to extinction predictions (Lomolino 2001; R. Freckleton 2005, personal communication), perhaps because the value of c is difficult to interpret. Values of c vary markedly among taxa and geographical locations (Connor & McCoy 1979; Rosenzweig 1995). Although c itself does not enter into most SAR calculations (it is assumed to remain unchanged following area loss, and cancels out of the equation), the 'slope' of the SAR is in reality a function of both z and c , and the two values show a tight interdependency (Rosenzweig 1995; Lyons & Willig 1999). To a large extent, c values reflect 'background' species

richness in the habitat matrix, and there are good reasons to expect that, rather than remaining constant, c will decline (and z increase) if habitats are fragmented, and if background levels of species richness decline. Such shifts would lead to species richness decreasing further than would be expected under the assumption that species–area curves remain ‘static’ over time (Lomolino 2001).

Uncertainties in habitat loss and the appropriate value of z can at least be addressed by generating a range of extinction predictions using different values for A_{future} and z . However, the uncertainty introduced by some related problems is less easily measured. First, what constitutes habitat loss? Many human impacts represent habitat modification or degradation rather than outright destruction; many species are likely to persist in (for example) the secondary forest that sometimes grows up following logging of rainforests. Second, z values vary at different spatial scales, and among different taxonomic groups, and thus the use of a single z value to characterize extinctions may be inappropriate. Third, applying the SAR to habitat loss requires the assumption that a single uniform block of habitat with species spaced evenly through it is reduced to another single (but smaller) habitat block (Simberloff 1992). In reality, habitat destruction rarely happens like that. Species richness is highly heterogeneous within and between habitats, and overall levels of extinction could be greatly increased or decreased, depending on the spatial distribution of species’ ranges and the actual pattern of habitat loss (Pimm & Raven 2000). In such circumstances, the use of a related approach, the endemic–area relationship (Harte & Kinzig 1997; Kinzig & Harte 2000) may lead to more accurate extinction projections. These will typically be lower than those for the SAR method, since the endemic–area method assumes zero relaxation: the only species to be lost are those whose entire range is destroyed.

Given these questions, finding a way to test the predictions of SAR estimates would be extremely useful. Such a test is impossible on a global scale, but can be attempted for regional-level estimates of extinction. Brooks *et al.* (1997) found a good correspondence between the number of endemic birds predicted to go extinct on individual south-east Asian islands using SAR calculations and information on the extent of deforestation, and a second estimate of extinction risk (from the Red Data Book listings of endangered species on each island). Unfortunately, the logic of this test is somewhat circular because the degree of habitat loss (the variable entered into the SAR calculation) is likely to be a key factor determining whether species on each island are listed as threatened. If sufficient time has elapsed to allow relaxation following habitat loss, a retrospective test of SAR predictions is possible. One such study, on woodland birds in Eastern north America, shows a good correspondence between SAR predictions and recorded extinctions (Pimm & Askins 1995; see also Kinzig & Harte 2000).

An alternative and overlooked method of testing SAR predictions is through experimentation. Replicated, manipulative experiments have a special role in

ecology and other sciences because they allow unambiguous testing of hypotheses. Clearly, experimental habitat reduction cannot be carried out on a geographically relevant scale because of ethical and practical limitations, although some fairly large-scale fragmentation experiments have been carried out, notably the Biological Dynamics of Forest Fragments project in the Brazilian Amazon (Laurance *et al.* 1997), with experimental fragments of forest ranging in area from 1 to 10 000 ha. However, these experiments have been hampered by low levels of replication and because relaxation is still likely to be in progress for many of the species under investigation. An alternative, smaller-scale approach using moss ‘microecosystem’ (Gonzalez *et al.* 1998; Gonzalez & Chaneton 2002), where the scale of study is appropriate to the dispersal ability of the organisms under study and where their generation times are sufficiently short for ‘relaxation’ to occur within the timescale of a 3 year research project, has proved highly successful and has the potential to further our understanding of the extent to which habitat loss causes extinctions. What remains debatable is the extent to which such results are relevant to the situations and scales of interest to conservationists.

3. APPLYING THE SPECIES–AREA RELATIONSHIP APPROACH TO CLIMATE CHANGE

The SAR method for predicting extinctions has generally been applied to habitat lost as a consequence of direct human habitat destruction. But if climate change alters the area and location of habitat available to a species, then with a little modification it may be possible to use the same general approach to predict extinctions likely to result from changes in climate. In fact, Thomas *et al.* are not the first to apply the SAR method to climate change-induced extinctions. Although not cited by Thomas *et al.*, over a decade earlier McDonald & Brown (1992) predicted the extent to which montane forest habitats in the Great Basin of the USA would decline under a scenario of a 3 °C rise in mean temperatures. They then applied a species–area curve based on contemporary patterns of montane mammal diversity to estimate how many species would remain in each montane forest following warming.

Thomas *et al.*’s calculations use a slightly different approach, based on the ‘climate envelope’ describing the environmental conditions suitable for each species to survive. As the climate warms, the climate envelope will shift in space. It may shrink in size, creep towards the poles, or retreat up mountainsides. The authors use the climate change predictions of climatologists to calculate what the distributional area of 1103 species from a variety of taxonomic groups and geographical locations is likely to be in the future, under different assumptions about the ability of species to track shifting climates (figure 2). The optimistic, full dispersal scenario is that the new distribution of each species will reflect the spatial extent of its new climate envelope. The pessimistic, zero dispersal scenario is that species will persist only in areas of overlap between current and predicted future distributions; in cases where there is no overlap these species will go extinct.

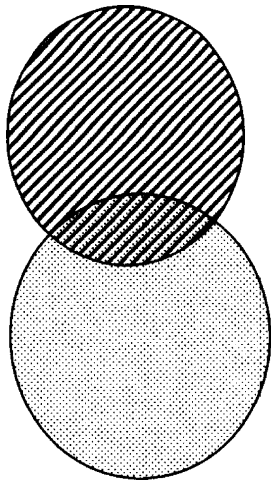


Figure 2. Schematic representation of range reduction under climate change. The outlines represent the climatic envelope suitable for a species to persist currently (stippled) and in a future, warmer world (hatched). The hatched area represents the future distribution of the species with global dispersal. The hatched and stippled area represents the future distribution with zero dispersal.

In reality, the response of most species will lie somewhere between these two extremes, and will depend on the dispersal ability of individual taxa, relative to the speed and magnitude of shifts in their climate envelope. Thomas *et al.* then use the habitat area change predictions in species–area calculations, using three slightly different approaches. First, they use changes in likely habitat area summed across species. Second, they use the proportional loss of habitat area averaged across all species. Finally, they use the change in each species' distributional area individually. All three methods generated broadly similar results: combining the different climate change and dispersal scenarios the number of species predicted to go extinct is estimated to range between 9 and 52%, with considerably lower extinctions predicted under minimal warming scenarios compared with mid-range and maximum warming scenarios.

Earlier, I listed some of the uncertainties in using the SAR model to predict extinctions. The application of SAR methods to climate change adds an additional, initial set of uncertainties. For a start, we cannot be sure precisely what future climates will be. A discussion of the science underpinning meteorological models of climate change, and the alternative models of economic growth on which these predictions are themselves based, is outside the scope of this review. As for uncertainties about the rate of habitat loss, the implication of different scenarios for extinctions can be explored (e.g. Thomas *et al.* 2004a). More problematic are a set of uncertainties concerning the usefulness of climate envelope models for predicting ranges under different climate change scenarios. If our predictions of future distributions for individual species (and thus of changes in effective habitat area) are uncertain, then the estimates that result from the SAR calculations will be doubly so. These issues have been discussed in detail elsewhere (e.g. Pearson & Dawson

2003; Hampe 2004; Pearson & Dawson 2004), but I highlight here some of the key areas of disagreement.

First, there is uncertainty about how many species have distributions truly governed by climate, and to what extent current distributions reflect the limits of climate tolerance. Most climate envelope case studies, including most of those used by Thomas *et al.*, use current distributions (realized niches) as the best available indication of climatic requirements. These models assume that current distributions are in approximate equilibrium with current climates. The widespread ability of species to persist if transplanted or introduced outside their current range and simulated climatic envelope suggests that this is often not the case (Hampe 2004). One factor that may lead to a mismatch between climatic conditions and species distributions is the fact that all species are embedded in a complex web of mutualistic and antagonistic interactions with other organisms. These interactions result in realized niches that are considerably narrower than the fundamental niches that a species can occupy in isolation, and are likely to differ from the realized niches that a species can occupy in a different community context (Pearson & Dawson 2003). 'Alien' plants and animals often thrive when introduced into areas outside their natural range, where predators, parasites, pathogens or competitors may be absent (Hampe 2004). Laboratory experiments on responses to climate change suggest that species will indeed respond differently in the presence of competitors and natural enemies (Davis *et al.* 1998). Inevitably, the distributional responses of species to climate change will be idiosyncratic, so that the set of interacting species present at any particular locality will not be a simple reconstruction of the community composition observed at other localities before climate change (Walther *et al.* 2002). The critical issue is the extent to which ability of a species to achieve long-term positive population growth rates (births + immigrants > deaths – emigrants) is affected by the abundance and identity of other species in newly assembled communities following climate change. This in turn may depend on the relative importance of 'diffuse' interactions (weak interactions with many co-occurring species) and stronger, pair-wise interactions with one or a few other species in influencing demography (Thomas 2005, personal communication). At present, the evidence needed to judge which of these situations is more typical is lacking.

A further question about the climate envelope approach involves the likely importance of adaptation (Harte *et al.* 2004). Optimists suggest that many organisms, particularly short-lived ones, may be able to evolve rapidly enough to adapt to changing environmental conditions, as seems to have occurred in some insects (Thomas *et al.* 2001) and for at least one species of plant grown outside its natural range for 8 years (Woodward 1987). Pessimists suggest this is unlikely: evolving to exploit marginal climatic conditions at the range margin may be inhibited by low levels of genetic variation, or because local adaptation is slowed by gene flow from the larger, core populations not experiencing the same directional selection (Davis & Shaw 2001; Thomas *et al.* 2004b). A final complication arises because different modelling

approaches can produce widely differing estimates of projected extinctions (Thuiller *et al.* 2004a,b), but this layer of uncertainty can at least be quantified and incorporated into the range of extinction predictions. Ultimately, even if individual species show distributional shifts that are idiosyncratic, it may still be valid to use mean distributional changes averaged over species, provided that the climate envelope method does not consistently overestimate or underestimate changes to species' distributions (Thomas *et al.* 2004b). It remains to be seen whether this requirement is met.

In their original paper, Thomas *et al.* indicate that the calculated extinction probabilities were specific to the regions and species included in the study, but also interpret their results as though they are global estimates. Earlier, I distinguished between two scales at which SAR extinction calculations have been attempted: regional and global. Using the Thomas *et al.* study to predict global extinctions merges these two scales of assessment. Even if predictions for the specific taxa and regions included in the study are accurate, the extrapolation to a global scale may be misleading. The set of species included in the analysis, although taxonomically and geographically diverse, is far from a random selection of the earth's species. In particular, in order to model the entire range of species, Thomas *et al.* necessarily limit their analysis to endemics, whose current ranges are entirely within the particular study areas. This automatically restricts the analysis to species with fairly small geographic ranges (small enough to be encompassed by individual study areas). It is well known that species with small geographic ranges are particularly prone to extinctions (Lawton 1995) and inevitably will be more likely to lose all or a substantial fraction of their distributions in a warmer world. Although Thomas *et al.* point out that most terrestrial species have range sizes that are smaller than their study areas, species whose ranges fall *entirely* within individual study areas (and do not overlap any of the study area's boundaries) are likely to be ones with particularly small ranges. Furthermore, only a small fraction of the species included by Thomas *et al.* are from tropical forests, but these forests account for over 50% of terrestrial biodiversity (perhaps considerably more) and may be less affected by climate change than habitats at higher latitudes (Sala *et al.* 2000).

It is worth noting that Thomas *et al.*'s methods will inevitably detect extinctions. Negative changes in the size of a species' range contribute to an increased extinction risk overall, while positive changes have no net effect on extinctions. Clearly, positive changes in diversity globally can only occur if there is speciation, but locally, the net effect on diversity at any one locality might well be positive, as species spread towards the poles from the most species-rich habitats near the equator (Buckley & Roughgarden 2004). It is also worth considering a thought experiment where global temperatures are maintained at the 2050 level for sufficiently long for all the extinction debt to be repaid. If we are then able (perhaps through new technology) to return temperatures to current or pre-industrial levels then the negative temperate shift resulting from this correction will inevitably cause an additional extinction spasm.

4. IS THERE A BETTER WAY?

The beauty, but also the limitation, of the SAR method applied to both habitat and climate-related extinctions is that detailed study of the ecology of individual species is not required. The approach is both general and flexible, but this makes it easy to overlook the multiple, interacting assumptions and uncertainties involved. Is there a better method for predicting the extent of future extinctions? Several other approaches have been used to predict the magnitude of the extinction crisis (Mace 1995), and some of these can be applied to climate change.

In their paper, Thomas *et al.* use one of these methods, based on International Union for Conservation of Nature and Natural Resources (IUCN) Red Data book criteria. Individual species were assigned to a IUCN threat category depending on the projected decline in their habitat area over 50 or 100 years, so that species with a projected future distribution of zero were deemed to have gone extinct, species with projected future distributions less than 10 km² or declining by 80% or more were allocated a 75% probability of extinction, and so on. Thomas *et al.* (2004b) also re-analysed part of their data using a far simpler extrapolation that also does not involve the species-area curve: by estimating how many species would lose all of their range areas. The two methods gave results broadly consistent with the SAR calculations.

Arguably these methods have even less biological justification than the SAR approach because of the assumptions they make about the ability of species to persist in small refuge habitats (Thuiller *et al.* 2004a). The information needed to make judgements about the minimum area of habitat critical to support individual species that would be needed to make these methods more accurate is unavailable for almost all of the earth's species, and certainly for those that constitute the bulk of global biodiversity: tropical invertebrates. Furthermore, we do not know what their current ranges are with any precision, and we are certainly not in a position to predict their future ranges. We must also be careful not to treat these methods as independent estimates of extinctions against which the SAR calculations can be compared or calibrated, because they use much of the same information and are subject to many of the same limitations.

A rather different, but potentially promising way forward is to accept the uncertainties inherent in any estimates of future extinctions, but to deal with these uncertainties explicitly using a decision-theoretic framework. Such an approach has the potential to bridge the gap between science and policy, and is being used increasingly in conservation contexts (e.g. Gerber *et al.* 2005). Scientists are used to dealing with uncertainties such as those about extinctions predictions, but for policy makers uncertainties about science are often perceived rather differently, delaying acceptance that policy changes are required, and at worst being used as an excuse for procrastination (Bradshaw & Borchers 2000). A formal decision-theoretic approach has the potential to make explicit the likely consequences of inactivity on climate change relative to other human impacts.

5. CONCLUSIONS

I began this review by describing the prediction of extinctions as more than just an academic exercise. Academic ecologists are in general unused to seeing their work in the public arena, and defending it to non-scientists—but they should not be surprised that dramatic estimates of extinctions, whether from climate change or other human activities, provoke strong responses. It is a bleak vision of the future that fewer than 50% of the species extant today might have viable populations by 2050, and such a major loss of diversity is difficult to imagine. However, just because it seems unlikely does not mean that it is impossible: compared to the very visible impact of tropical deforestation and other habitat loss, climate change is an insidious change that threatens to creep up on us unawares. Certainly, the direst predictions of climatologists (global temperatures within 100 years higher than any the earth has experienced within the last 2 million years) would cause innumerable extinctions. However, the layers of uncertainty I have described should be sufficient to make us very wary of the accuracy of the existing extinction predictions under more modest and gradual climate changes, particularly in the context of the climatic and fossil records. Marked variations in climate over the last 10 000 years (including extended periods when global temperatures have increased or decreased to a greater extent than the minimum warming scenario investigated by Thomas *et al.*, and at a similarly rapid rate) have had relatively little impact on extinctions (e.g. Coope 1995; Davis & Shaw 2001); and where species have gone extinct the effect may have been to ‘filter out’ those species most sensitive to climate change.

Unfortunately, it will be a very long time before we are in a position to judge the accuracy of most extinction predictions, and by then it will be too late to do anything to prevent them. For applications of the SAR model to conventional habitat loss, it is possible to validate the predictions by using independent measures of extinction probability, or by carrying out small-scale experiments. In contrast, there is no obvious way of validating climate change predictions: only time will tell. Even in 2050, the cut-off point used by Thomas *et al.* and others in their analyses, we will have only a slightly better idea of their accuracy. Range changes for most species will not have reached equilibrium with the climates current at that time, and even when they do, there will be a further time delay before population sizes reach equilibrium. A frequent criticism of claims that climate change will be a major cause of extinctions is that despite almost a century of warming only a handful of species are currently known to have gone extinct as a consequence of climate change. This ignores the difficulties (and strict criteria) needed to confirm extinctions, and to confirm that climate change is their cause; but more importantly it overlooks the inevitability of an extinction debt.

If climate change is accepted as a genuine and immediate threat to biodiversity we do need to reduce emissions of carbon dioxide and other greenhouse gases, and to develop technologies for greenhouse gas sequestration, as Thomas *et al.* suggest, although it is the wider economic impacts of climate change, rather

than concerns about biodiversity, that seem most likely to stir governments to action. On the day I write these words (16th February 2005), The Kyoto Protocol, aimed at curbing greenhouse gas emissions, has come into force. Under the best-case scenario, carbon dioxide levels in the atmosphere will continue to rise, and so will global temperatures. Thus, we also need to find ways to minimize and to mitigate the effects of climate change on biodiversity. Such mitigations are unlikely to be as straightforward as those necessary to slow the loss of species from habitat destruction, but because climate change and habitat loss are likely to interact to increase extinction rates above the level expected if each acted alone, a continuing focus on habitat protection, particularly on a landscape scale, seems a sensible priority for conservationists. Habitats are required where species currently occur, in locations where they may move in future, and also in intermediate areas that they will have to traverse. While an uncritical interpretation of the Thomas *et al.* paper might suggest that the traditional focus of conservationists on habitat protection and management are of decreased importance, Thomas (2005, personal communication) believes that, to meet these requirements, more habitat conservation is required in the context of climate change, not less. It would be very unfortunate if a focus on limiting climate change led to a reduced investment in habitat protection.

Any attempts to calculate the likely magnitude of future extinction inevitably have a back-of-the-envelope feel to them. The logical simplicity of the SAR method conceals a hotchpotch of assumptions, extrapolations, approximations and estimates that combine to generate considerable uncertainty, rather more than can be adequately indicated within the restrictions of a *Nature* paper. While I have discussed the SAR method in some detail, the debate over its validity is only one aspect of a series of considerations which lead to uncertainty about the likely magnitude of extinctions caused by climate change. Thomas *et al.* (2004a,b) tend to emphasize the factors that may make their prediction of future extinctions too low. Here I have instead concentrated on factors that may make their predictions too high, as well as those that add in uncertainty in either direction. To their credit, Thomas *et al.* (2004a,b) accept and make explicit many of the issues I have discussed, and have stated that the article provides a ‘first pass’ estimate at global extinctions. In the coming decades, how can the accuracy of our ‘second pass’ and subsequent estimates be improved? For me, use of the SAR approach is unlikely to provide us with more accurate answers. Like Harte *et al.* (2004) I am more comfortable with estimates of extinction calculated on a species-by-species basis, but such estimates are hampered by our almost total ignorance of the minimum critical habitat required by most species, particularly the small, poorly studied ones living in the most diverse habitats on earth, the tropical forests. This makes extrapolating from the inevitably small sets of species for which such data exist to global extinction estimates problematic. These approaches also still suffer from a variety of the uncertainties I have

discussed, notably those associated with the use of climate envelopes.

Faced with such problems, is estimating extinctions really a worthwhile task? For me, the major usefulness of such exercises is in destroying any residual complacency about climate change among conservationists and hopefully among policy makers, and in highlighting that a conservation strategy based on a static and isolated set of parks or reserves is unlikely to be robust to global climate changes. My major concern is that a new focus on climate change might lead to a too-radical reshaping of conservation policy and spending, such that the current and ongoing onslaught of habitat destruction, particularly in the tropics, is neglected. Rather than seeking to make ever more accurate predictions of extinctions, the real challenges for conservation biologists in the coming decades will be to find a way to partition extinctions among particular causes and their interacting effects, allowing us to prioritize the allocation of resources to different human impacts and to identify and implement the practical means to slow the rate at which species go extinct.

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