Population and geographic range dynamics: implications for conservation planning

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Continuing downward trends in the population sizes of many species, in the conservation status of threatened species, and in the quality, extent and connectedness of habitats are of increasing concern. Identifying the attributes of declining populations will help predict how biodiversity will be impacted and guide conservation actions. However, the drivers of biodiversity declines have changed over time and average trends in abundance or distributional change hide significant variation among species. While some populations are declining rapidly, the majority remain relatively stable and others are increasing. Here we dissect out some of the changing drivers of population and geographic range change, and identify biological and geographical correlates of winners and losers in two large datasets covering local population sizes of vertebrates since 1970 and the distributions of Galliform birds over the last two centuries. We find weak evidence for ecological and biological traits being predictors of local decline in range or abundance, but stronger evidence for the role of local anthropogenic threats and environmental change. An improved understanding of the dynamics of threat processes and how they may affect different species will help to guide better conservation planning in a continuously changing world.

Keywords: threat drivers; population abundance; geographic range contraction; extinction risk; conservation planning; range dynamics

1. INTRODUCTION

For many years conservation organizations and government agencies have worked to identify, prioritize, manage and restore wild species and habitats. This work was given an added focus and emphasis by the commitment made by governments in 2002/2003 to 'reduce the rate of loss of biodiversity by 2010' (SCBD 2003; Balmford *et al.* 2005). However, as various recent audits make clear, this target has not been met. At species and population levels biodiversity continues to decline, often at increasing rates (Butchart *et al.* 2005; Collen *et al.* 2009).

Biodiversity decline is of concern for several reasons. Most immediately, many people depend directly on biodiversity for food, fibre, fuel and medicines. While more developed societies are buffered from such direct dependence, everyone ultimately relies on healthy ecosystems that will continue to function and support ecosystem services even in the face of rapid environmental change (Díaz *et al.* 2006). To a greater or lesser degree, ecosystem functions depend upon biodiversity (Naeem *et al.* 2009). Beyond these utilitarian and functional roles,

biodiversity matters for ethical and aesthetic reasons. The richness and diversity of nature are valued for its own sake by people everywhere. The components of biodiversity that contribute to these different roles will not necessarily be the same, but all are important and together they provide strong reasons to be concerned about the continuing high rates of biodiversity loss.

A better understanding of biodiversity loss and change is necessary for developing and implementing conservation policies, most notably because it is unlikely that declining biodiversity trends can be reversed while the processes responsible are still in place (Mace & Baillie 2007; Butchart *et al.* 2010). As well as the direct effects that people have on species, we are in a period of rapid environmental change, with land-use change, the impact of people on the oceans, and climate change underway at higher rates than at any other time in human history (Millennium Ecosystem Assessment 2005). Environmental changes affect species viability, leading to local extinctions, and to emigration and immigration with consequent changes to both the diversity and composition of ecological communities. Because some species respond more rapidly than others, there are inevitably transient as well as permanent changes to local biodiversity (Tilman *et al.* 1994; Jackson & Sax 2009). The transient effects may persist for considerable periods of time;

extinction debts, for example, may have half-lives of decades to centuries (Brooks *et al.* 1999; Vellend *et al.* 2006). Immigration rates may be slow and dependent on chance events, but may also be quite rapid as seen in the apparent tracking of many contemporary species to ongoing climate change (Parmesan & Yohe 2003). The consequences of this include shifts in the composition and structure of communities affecting both ecological and functional attributes.

Many of the current trends may be hard to reverse quickly because both the processes driving biodiversity declines and many features of natural systems have significant barriers to change and time lags (Jackson & Sax 2009). For example, efforts to reduce the impact of fisheries on marine fish populations are hindered by both the time and effort needed to change the behaviour and activities of fishing communities as well as to accommodate the long generation times of some commercially fished species (Pauly *et al.* 1998). Lag times may be relevant for other kinds of threats to species, such as over-exploitation, the impacts of invasive species, habitat loss and land-use change and, of increasing importance and relevance, climate change (Armbruster *et al.* 1999; Frankham & Brook 2004; Chevin *et al.* 2010).

So far, reporting of biodiversity loss has tended to be of aggregated rates of change in population sizes (e.g. Loh *et al.* 2005; Scholes & Biggs 2005), species threat levels (e.g. Butchart *et al.* 2005) and geographic range size (e.g. Jetz *et al.* 2007), averaged across all the entities being measured. This averaging can hide important variation. While some species or populations might be in rapid decline, others might be stable or even increasing. The characteristics of the declining species or populations will influence the impacts of species losses on ecological communities and on ecosystem functions. For example, there is theoretical and empirical evidence that species occupying the highest trophic level are more vulnerable to extinction than those at other trophic levels (Petchey *et al.* 1999; Purvis *et al.* 2000; Dobson *et al.* 2006), and therefore once lost locally, any top-down control they exert over the composition of lower trophic levels could be compromised. Rapid environmental change can favour rapidly reproducing generalist species, leading to marked changes in community composition and ecological roles (Sekercioglu *et al.* 2004; Laurance *et al.* 2006).

Here, we explore the patterns and sources of variation in rates of decline in two large species-level datasets. Specifically, we investigate the following questions:

— To what extent do the average trends reported for aggregated data hide variation among species?
— Do species decline consistently across different time periods?
— Are there consistent geographical, ecological or life history correlates of declining, stable or increasing abundances or geographical distributions?

2. METHODS
(a) *Datasets*
(i) *Geographic range dynamics in Galliformes*
This dataset includes the 127 species of the avian order Galliformes (pheasants, partridges, quails, etc.)

found in the Palaearctic and Indo-Malay biogeographical realms. Point locality data, accurate to within 30 miles (approx. 50 km) were collected from a variety of historical and present-day sources—museum collections, journal articles, personal reports and letters, ringing records, ornithological atlases and birdwatching trip-report websites (Boakes *et al.* 2010*b*). The database contains 79 701 records suitable for use in this study, dating from 1727 to 2008.

Although the dataset was compiled as comprehensively as possible, recording effort is unavoidably uneven (Boakes *et al.* 2010*b*) making absolute comparisons of geographic range changes difficult to interpret. To compensate for changes over time in both recorder effort and geographical coverage, we used a relative index of change that works by calculating relative geographic range change between two time periods for each species relative to the group as a whole (Telfer *et al.* 2002). We aggregated the point locality data into a Behrmann equal area projection, using a grid with cells measuring 48.24×48.24 km, approximating to a half degree resolution. To control for change in geographical coverage with time, only cells that were surveyed in both of the time periods being compared were included. The number of grid cells containing one or more records was counted for each species in each time period. Only species with a minimum of five cells in the early period were included in the analysis to avoid curvilinearity; for the rarest species there is far greater capacity for expansion than for decline. These grid cell counts were then expressed as proportions of the total survey area and logit-transformed. A linear regression model was fitted to the logit-transformed proportions from the earlier and later periods and weighted to account for heteroscedasticity. Each species' standardized residual was then taken to represent an index of its change in geographic range size, relative to the trend in the whole group. Full details of the method are in Telfer *et al.* (2002). The standardized residuals represent relative change only. If all of the species in the group were declining, a positive residual would still represent a decline, albeit a smaller one relative to the group as a whole than that represented by a negative residual.

(ii) *Vertebrate population abundance*
Data on trends in vertebrate abundance spanning the period 1970–present were drawn from the Living Planet Index database (www.livingplanetindex.org) (see Loh *et al.* 2005; Collen *et al.* 2009). Data include time-series information for vertebrate species from published scientific literature, online databases including the Global Population Dynamics Database (http://www. sw.ic.ac.uk/cpb/cpb/gpdd.html) (Inchausti & Halley 2001), the Pan-European Common Bird Monitoring (2006) and non-Governmental Organization and National Park records. Data are only included if (i) a measure of population size is available for at least 6 years, (ii) information is available about how the data were collected and the units of measurement are clearly specified, (iii) the geographical location of the population is provided, (iv) the data were collected using the same method on the same population throughout the time

series, and (v) the data source is referenced and traceable (Collen *et al.* 2009). We further refined these data to only include populations with a span of greater than 10 years, resulting in a dataset of 158 271 annual abundance estimates of 10 566 populations from 2547 species.

To calculate comparable measures of change in population abundance over time, we followed Collen *et al.* (2009) and used a generalized additive modelling (GAM) framework. Calculations were carried out using the MGCV package (Wood 2006) in R v. 2.11 (R Development Core Team 2006). A GAM framework might be advantageous in long-term trend analysis because it allows change in mean abundance to follow any smooth curve, not just a linear form (Fewster *et al.* 2000). The GAM method has greater flexibility for drawing out the long-term nonlinear trends than chain or linear modelling methods. Using these models, we calculated a log annual relative rate of change in population size in each year. Species values were calculated from the annual rate of population change by calculating a geometric mean value.

For each of the two datasets we also collated information on certain biological traits that might predict change in status of both range and abundance. We evaluated body size (above or below median value), geographic range size (above or below median), region (temperate or tropical), habitat (forest or non-forest) and altitude (montane or lowland). Galliformes data were compiled from Boakes *et al.* (2010b), and owing to data availability, data for the vertebrates represented in the population abundance database were restricted to mammals, and compiled from Jones *et al.* (2009).

(b) *Analyses*
(i) *Time periods for comparison*
The nature and intensity of drivers of biodiversity change have altered with time and so we examine whether patterns of population or range change are similar across different time periods when different drivers have predominated. The Galliformes sightings were compared between four time periods: pre 1900, 1900–1949, 1950–1979 and 1980 onwards. In addition, both the Galliformes geographic range change and the population abundance trends were compared pre- and post-1980 since several lines of evidence suggest a rapid escalation of anthropogenic processes affecting species and habitats after about 1980 (Millennium Ecosystem Assessment 2005).

(ii) *Tests*
For each dataset and within time periods the degrees of change observed in different species were ranked and plotted to display the range of changes. We implemented Wilcoxon's matched pairs tests in order to evaluate whether the same species show similar relative levels of decline across different time periods. For both datasets matched pairs were calculated only for those species that were used in all time comparisons. Wilcoxon signed-rank tests were used to investigate traits that might predict changes in range or abundance. All tests were carried out in R v. 2.11 (R Development Core Team 2006).

3. RESULTS
1. To what extent do the average trends reported for aggregated data hide variation among species?

The two datasets show a similar pattern in that only a few species exhibit large changes in either range size or abundance (figure 1). Simple measures of central tendency manifestly hide important variation in geographic range and population trends over time. Changes in geographic range size in the Galliformes show a less pronounced pattern than the abundance data, with relatively few species showing large range changes relative to the rest of the group. This effect might be partially attributable to the method used owing to the absence of information on sampling effort (see §4).

2. Do species decline consistently across different time periods?

Across both datasets species do not generally show systematic patterns in decline rates over time, with marked declines or increases within one time period for species not necessarily being reflected in other time periods (table 1). In the population abundance data, the matched pairs analysis shows that across species changes in abundance values in the first time period (pre-1980) are significantly different from those in the second time period (post-1980; table 1). Significant differences were not seen for the relative range changes. Of the species that could be included in each of the comparisons pre-1900 to 1900–1949, 1900–1949 to 1950–1979 and 1950–1979 to 1980 onwards, only seven show consistently positive range changes relative to the group while only four show consistently negative changes.

3. Are there consistent geographical, ecological or life history correlates of declining, stable or increasing abundances or geographical distributions?

Among the Galliformes, we found several significant predictors of relative range change (table 2) although none of these was consistent over time. Species with below-median geographic range size and species with above-median body size suffered significantly less relative range change post-1980 compared with pre-1980. The same relationship was found for species from forest and montane habitats. These traits were also found to be significant for at least one other time-comparison but not across all time periods. The inconsistency of the effects could in part be explained by a lack of survey data in some time periods, notably 1950–1979. Neither lowland forest nor tropical/temperate habitats were found to be significant predictors for any of the time comparisons. For the abundance data, we restricted the analysis to mammals in order to compare predictive traits (table 3) and found that small body size was significantly associated with declining abundance in tropical mammals in the pre-1980 data period ($W = 2405$, $p < 0.05$). None of the other predictors tested showed significant associations with abundance trend over either time period.

(a) *Methodological caveats*
A number of methodological issues may affect our results. First, although the Galliforme data were
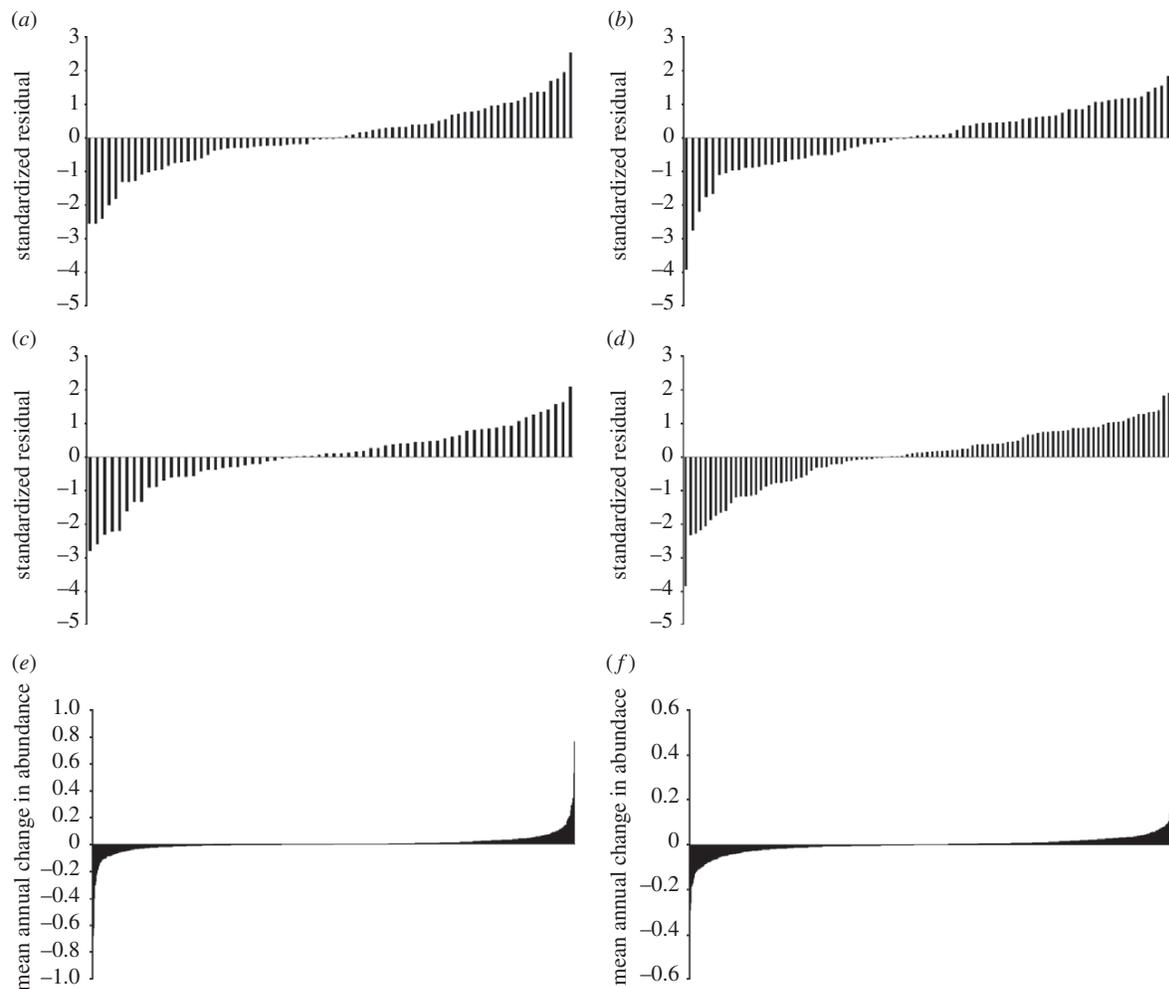
Figure 1. Distribution of relative change in range size for Galliformes for (*a*) pre-1900 to 1900–1949, (*b*) 1900–1949 to 1950–1979, (*c*) 1950–1979 to 1980 onwards, (*d*) pre-1980 to 1980 onwards, and relative change in vertebrate population abundance for (*e*) 1970–1980 and (*f*) 1981–2007. Each bar represents the change shown by a single species relative to the rest of the group (Galliformes) or the mean annual change in population abundance by species (vertebrates).

systematically collected from all available sources, this cannot take account of biases in recording and documenting, which have demonstrably changed with time (Boakes *et al.* 2010*b*). Similarly, although the abundance dataset is as comprehensive as possible, there are inevitable biases that result from the compilation of time-series data that primarily come from published resources (see Collen *et al.* 2009), specifically a dominance of better studied, large-bodied, commercially important or temperate species. We indicate below where these biases might affect our results and conclusions.

Difficulties in comparing records over time meant we were restricted to using relative changes in the geographical distributions of Galliformes. Telfer *et al.*'s (2002) method assumes that recorders record all species that they see, hence allowing for recorder competency to change over time. However, results can be affected should effort towards a particular species or group of species change. It is clear that there has been increased attention towards threatened species of Galliformes in recent times

(Boakes *et al.* 2010*b*) so it is possible that our results could underestimate any range declines they may have suffered. The restriction of the analysis to areas that have been sampled in both time periods may also lead to an underestimation of range decline. Habitat that has been urbanized or otherwise converted between the two periods may not have been revisited in the later period and hence any such potential range losses will be excluded from the analysis. The exclusion of species with initial ranges of fewer than five cells might also lead to a falsely positive picture since species that decline to this level will drop out of the analysis over time although, conversely, species that undergo range expansions could balance this effect. A closer examination of the data shows that the number of species dropping out of the analysis was approximately equal to the number added in due to their ranges expanding to five cells or more. It therefore seems reasonable to conclude that these additions and losses did not have any directional effects on the results.

Table 1. Wilcoxon's matched pairs results of comparison of species values of vertebrate abundance and change in range size of Galliformes between time periods. Bold indicates significance at the 5% level.

	time period comparison	V	n species	p
vertebrate abundance	pre-1980—post-1980	367 100	1329	**0.009**
Galliformes range size	pre-1900 to 1900–1949 compared with 1900–1949 to 1950–1979	651	47	0.363
	pre-1900 to 1900–1949 compared with 1950–1979 to 1980 onwards	729	47	0.082
	1900–1949 to 1950–1979 compared with 1950–1979 to 1980 onwards	639	47	0.434

4. DISCUSSION

Our results reveal strong variation among species and over time in the dynamics of species' geographic range sizes and population abundances. While global measures of biodiversity change derived from these cross-species datasets consistently show an overall decline (Collen *et al.* 2009; Butchart *et al.* 2010), at any one time, these average trends hide important variation among species, and the identities of species showing large changes might be more dynamic over time than previously thought.

Most species in our datasets show rather little variation in abundance between years, with only a small number showing marked increases or decreases in abundance or geographic range size. It is well known that species populations fluctuate over time and that this can be driven by intrinsic dynamics. However, while there is theoretical and empirical evidence that temporal variability in populations is related to the length of time over which it is measured and that stability is related to life history (Inchausti & Halley 2001; Sibly *et al.* 2007), these are relatively small effects, suggesting we must look to extrinsic processes to explain the larger changes we observe in the data analysed here. The subsets of species showing rapid change could be those that have life history and/or ecological traits that make them especially prone to decline, and/or could be those experiencing some new extrinsic pressure. In the former case, we would expect to see consistent relationships across time periods in the identity, life history or ecology of species with high and low rates of change.

In fact, our analysis revealed few biological predictors of change in abundance and range, and where

Table 2. Predictors of change in range size for Galliformes over time. Values represent outcome of Wilcoxon's signed-rank test. For clarity, significant *p*-values (*p*) are highlighted in bold. Superscript a or b indicates the trait that is associated with declining range.

predictor	pre-1900 to 1900–1949 W	p	pre-1900 to 1950–1979 W	p	pre-1900 to 1980 onwards W	P	1900–1949 to 1950–1979 W	p	1900–1949 to 1980 onwards W	p	1950–1979 to 1980 onwards W	p	pre-1980 to 1980 onwards W	p
range size (above[a]/below median[b])	522[b]	0.905	303.5[b]	0.722	256[a]	0.532	574[b]	0.373	499[a]	**0.016**	510[a]	0.757	802[a]	**0.046**
body mass (above[a]/below median[b])	593[b]	0.636	290.5[a]	0.367	423.5[b]	0.062	614[b]	0.591	1188[b]	**0.001**	700[b]	**0.019**	1539[b]	**<0.001**
forest[a]/non-forest[b]	570.5[b]	0.9	250.5[a]	0.075	398[b]	0.259	544[a]	0.699	997.5[b]	**0.047**	559.5[a]	0.771	1319[b]	**0.05**
montane[a]/lowland[b]	352[b]	**0.01**	325[b]	0.688	241.5[b]	0.142	535[b]	0.071	616[b]	0.137	339[b]	**0.049**	804[b]	**0.046**
montane forest[a]/montane non-forest[b]	113[b]	0.126	98[a]	0.78	69[b]	**0.027**	190[b]	0.989	169[b]	**0.021**	195[b]	0.362	229[b]	**0.014**
lowland forest[a]/lowland non-forest[b]	152[a]	0.2	121.5[a]	**0.005**	59[b]	0.503	114.5[a]	0.694	115[b]	0.638	75.5[a]	0.341	170[b]	0.872
tropical[a]/temperate[b]	474.5[a]	0.519	299[a]	0.454	336.5[a]	0.912	564[b]	0.825	775[b]	0.808	428	0.143	982[b]	0.696
threatened[a]/non-threatened[b]	347.5[a]	0.114	161[a]	1	133.5[a]	0.529	268[b]	0.971	283.5[b]	0.107	220.5[a]	0.326	469[b]	0.079

Table 3. Predictors of change in abundance for vertebrates between 1970 and 1980 and post-1980 abundance trends. Values represent outcome of Wilcoxon's signed-rank test. For clarity, significant *p*-values are highlighted in bold. Superscript b or c indicates the trait that is associated with declining abundance.

	tropical species				temperate species			
	pre-1980		post-1980		pre-1980		post-1980	
predictor	W	p	W	p	W	p	W	p
body mass[a] (above[b]/below median[c])	2405[c]	**0.006**	1798[c]	0.18	1892[c]	0.25	1754[c]	0.69
range size[a] (above[b]/below median[c])	1777[c]	0.56	1739[c]	0.44	761[c]	0.58	871[c]	0.64
forest[b]/non-forest[c]	1507[b]	0.72	1375[c]	0.26	1691[b]	0.9537	1610[c]	0.71

[a]Analysis restricted to mammals.

we did find significant associations these were different in the two datasets. In the Galliformes, those species with relatively larger geographic ranges and relatively small body sizes were declining faster. This may be a consequence of very narrowly distributed species being relatively well protected. There may be more complex explanations for some of the observed patterns. For example, in recent periods in Japan, conservation measures have increased the area of mature forest, leading to declines in species colonizing new forest and an increase in mature forest specialists (Yamaura *et al.* 2009). It is possible that similar associations with habitat change over time may explain some of the patterns our data.

We found no evidence that species were consistently increasing or decreasing in range or abundance over time and very limited evidence for consistent association with ecology and life history. This suggests that the most significant contribution to range and population change in the species we analysed comes from extrinsic sources, i.e. from changing environmental pressures, anthropogenic threats and resulting changes in ecosystems and communities. It is well established now that over the past 50 years there has been more substantial change to habitats globally than at any other time in human history (Millennium Ecosystem Assessment 2005), and that the major drivers of change have varied and continue to vary in both nature and intensity over time and space (Sala *et al.* 2000; Millennium Ecosystem Assessment 2005; Mace 2010). Hence, the most probable explanation for the rapidly declining or increasing trends is as a result of the appearance or cessation of novel environmental changes and threats. Persistent threats will cause marked declines or the local extinction of species that are susceptible to them, while resilient species will persist, perhaps at increased abundance, especially if there are compensatory dynamics (Gonzalez & Loreau 2009).

Because species vary in their resilience to different threats, the appearance of a novel threat or driver will cause more rapid species loss or affect more species than will the continuation or repeated appearance of the same threat or driver, a process that leads to extinction filters (Balmford 1996). As the effects of invasive species, over-exploitation, habitat loss and now climate change become predominant in different areas and focus on different communities, we see their sequential toll on the fate of some species, but also the increasing abundance or recovery of some other, generally more resilient species. Locally this process may look like recovery or something close to stability, but regionally and globally it generally represents the loss and the global homogenization of biodiversity (McKinney & Lockwood 1999).

(a) The consequences of biodiversity loss

There is a consensus that biodiversity supports ecosystem functions and the greater the biodiversity the more options there will be to maintain function in a changing world. However, the links between biodiversity and ecosystem processes are poorly understood and highly variable depending on context (Diaz *et al.* 2007). In fact, for most well-understood ecosystem functions, the biodiversity contribution is better measured by functional traits rather than through measures of species richness or population abundance (Diaz & Cabido 2001). Had we shown strong associations between life-history traits and rapid declines, this could have indicated traits that were at relatively high risk, and thence functional attributes most likely to be lost. In fact, although there is some evidence in our analysis that certain biological traits make species more vulnerable to local decline or range loss, these are weak and inconsistent, especially compared with comparable analyses that have been undertaken at the species level.

Cross-species studies examining the biological correlates of high extinction risk have consistently highlighted low population density, small range size, low reproductive rates and slow turnover between generations as significant predictors (Owens & Bennett 2000; Fisher & Owens 2004; Cardillo *et al.* 2005, 2008). There are several possible reasons why we might not find comparable results in this analysis. First, in both our datasets we include a much less variable range of species, traits and patterns of decline. Given the probable variability in the relationships between decline and biological traits, it may be that our analysis is simply too preliminary and the data too coarse to identify any patterns that do exist. This in part results from using data gathered for different purposes. A more efficient approach would be to design sampling and monitoring systems that are suited to the purpose at hand (Green *et al.* 2005a). Secondly, it may be that different processes are significant in determining local population dynamics

compared with those associated with species-level extinction, and that the factors driving range loss are more strongly associated with environmental change than biological traits. In fact, a more detailed analysis of the population abundance data suggests that environmental variables are generally better determinants of cross-species population level decline rates than biological traits (Collen *et al.* in press). In general, there is no reason to suppose that local population processes affecting site-level abundance or range extent will scale up to the species level, even if ultimately the fate of species depends on the fate of constituent populations. However, given that much conservation activity is implemented at the population level, understanding these scaling processes is important.

The results here are preliminary but suggest that extrinsic drivers and threat processes are better predictors of range dynamics and local population declines than intrinsic biological traits. In future analyses these might be more easily linked to functional traits that simultaneously affect the ability of species and populations to persist, and deliver key ecosystem processes and functions. Understanding and predicting new threats and environmental change drivers will contribute to better predictions about places and taxa that are likely to soon suffer loss of abundance or diversity.

(b) *Implications for conservation planning*

In light of these findings, there are several implications for conservation planning. First, the preliminary study here indicates that averaged trends hide much variation among species, places and time periods. More will be learned by disaggregating these data and identifying the important causal factors at any particular time and place. It is clear that the future is not a straightforward projection of the past, so recent and historical trends cannot constitute robust predictions for the future. However, identifying the traits and characteristics of susceptible taxa, the changing focus of extrinsic pressures and threats and the interactions between these will indicate places and species that may next be most at risk (Cardillo *et al.* 2006; Davies *et al.* 2008).

The drivers of biodiversity declines have changed over time, leading to substantial shifts in the geographical and taxonomic focus of conservation activity, a trend that is likely to continue into the future. Evidence suggests that the majority of species that are currently declining in range extent and population size are responding to habitat loss (Vie *et al.* 2009). This is unlikely to slow given the apparent contagion of habitat decline (Boakes *et al.* 2010a). However, the traits that predispose species to an elevated risk of decline have been found to vary according to the threat (Owens & Bennett 2000; Isaac & Cowlishaw 2004; Price & Gittleman 2007) and so we must expect the focus of future declines to change. Emerging threats such as climate change will have interactive effects with the current drivers that are generally likely to increase overall risks (Brook *et al.* 2008). While the biological measures that indicate a predisposition to elevated extinction risk (e.g. small and declining population size, declining geographic range, slow life history (Mace *et al.* 2008))

are likely to remain significant whatever the threat, schemes to evaluate risk will need to continue to be re-assessed to ensure they reflect risks posed by emerging extrinsic threats and impending environmental change (Cardillo *et al.* 2006; Keith *et al.* 2008).

Certain trends are likely to continue into the near future. For example, land clearance for agricultural cropland and pasture has already reduced the extent of natural habitats on agriculturally usable land by more than 50 per cent (Food & Agricultural Organisation of the United Nations 2001), and world food demands are projected to double by the year 2050. Coupled with the fact that these impacts are likely to be greater in less-developed tropical countries (Green *et al.* 2005b), where biodiversity is greater (Hawkins 2001), this suggests that habitat loss and degradation will remain dominant even as climate change impacts grow over the coming decades (Jetz *et al.* 2007). Unlike the other threat processes, climate change is relatively new with different foci and consequences, but there are few observations on which to base future predictions. A potentially different suite of species from our study will be affected by climate change. In the Galliformes, for example, montane species are currently doing well, potentially owing to the fact that the land they occupy is relatively inaccessible, and habitat loss has been slow. This trend may not continue as montane habitats shrink owing to changing climate. New methods for identifying climate change impacts will be needed to generate meaningful information for conservation planning (Foden *et al.* 2009).

Existing protected area systems, the cornerstone of conservation efforts, are static though they must deal with dynamic threats (Visconti *et al.* 2010). With the population abundance of many species in protected areas now in decline (e.g. Craigie *et al.* 2010), future planning for conservation will need to be adapted to take into account these changing threats (Pressey 1994; Fuller *et al.* 2010). Although critically important to track the changing distributions of narrowly distributed species, dynamic conservation planning both inside and outside formal protected areas will also become increasingly important for the conservation of currently common and widespread species, which are by no means immune to declines of large magnitude (Gaston & Fuller 2008).

5. CONCLUSIONS

Rates of decline documented in cross-species and population datasets provide some of the most compelling evidence about the changing rates of global biodiversity loss. But the average rates reported hide significant variation among species and populations. Especially important for extrapolating these trends into the future is the observation that overall rates could be strongly influenced by a few populations or species exhibiting rapid change. Moreover, our finding that the identity of the most rapidly declining species varies over time, and the fact that we did not identify consistent ecological or life-history predictors of change, together suggest a strong role for local environmental change and threats in determining the trends. Adding yet more complexity, these causal processes

are also changing over time. Further disaggregation of these data will allow better insights into the processes that could next cause major population declines and range loss, and a better understanding of the interactions among threats, environmental change, species traits and habitat conservation could provide a basis for more efficient proactive conservation planning.

REFERENCES

Armbruster, P., Fernando, P. & Lande, R. 1999 Time frames for population viability analysis of species with long generations: an example with Asian elephants. *Anim. Conserv.* **2**, 69–73. (doi:10.1111/j.1469-1795.1999.tb00050.x)

Balmford, A. 1996 Extinction filters and current resilience: the significance of past selection pressures for conservation biology. *Trends Ecol. Evol.* **11**, 193–196. (doi:10.1016/0169-5347(96)10026-4)

Balmford, A. *et al.* 2005 The Convention on Biological Diversity's 2010 target. *Science* **307**, 212–213. (doi:10.1126/science.1106281)

Boakes, E., Mace, G. M., McGowan, P. J. K. & Fuller, R. A. 2010a Extreme contagion in global habitat clearance. *Proc. R. Soc. B* **277**, 1081–1085. (doi:10.1098/rspb.2009.1771)

Boakes, E., McGowan, P. J. K., Fuller, R. A., Chang-qing, D., Clark, N. E., O'Connor, K. & Mace, G. M. 2010b Distorted views of biodiversity: spatial and temporal bias in species occurrence data. *PLoS Biol.* **8**, 1–11. (doi:10.1371/journal.pbio.1000385)

Brooks, T. M., Pimm, S. L. & Oyugi, J. O. 1999 Time lag between deforestation and bird extinction in tropical forest fragments. *Conserv. Biol.* **13**, 1140–1150. (doi:10.1046/j.1523-1739.1999.98341.x)

Brook, B. W., Sodhi, N. S. & Bradshaw, C. J. A. 2008 Synergies among extinction drivers under global change. *Trends Ecol. Evol.* **23**, 453–460. (doi:10.1016/j.tree.2008.03.011)

Butchart, S. H. M., Stattersfield, A. J., Baillie, J. E. M., Bennun, L. A., Stuart, S. N., Akçakaya, H. R., Hilon-Taylor, C. & Mace, G. M. 2005 Using Red List Indices to measure progress towards the 2010 target and beyond. *Phil. Trans. R. Soc. B* **360**, 255–268. (doi:10.1098/rstb.2004.1583)

Butchart, S. H. M. *et al.* 2010 Global biodiversity: indicators of recent declines. *Science* **328**, 1164–1168. (doi:10.1126/science.1187512)

Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R. P., Sechrest, W., Orme, C. D. L. & Purvis, A. 2005 Multiple causes of high extinction risk in large mammal species. *Science* **309**, 1239–1241. (doi:10.1126/science.1116030)

Cardillo, M., Mace, G. M., Gittleman, J. L. & Purvis, A. 2006 Latent extinction risk and the future battlegrounds of mammal conservation. *Proc. Natl Acad. Sci. USA* **103**, 4157–4161. (doi:10.1073/pnas.0510541103)

Cardillo, M., Mace, G. M., Gittleman, J. L., Jones, K. E., Bielby, J. & Purvis, A. 2008 The predictability of extinction: biological and external correlates of decline in mammals. *Proc. R. Soc. B* **275**, 1441–1448. (doi:10.1098/rspb.2008.0179)

Chevin, L.-M., Lande, R. & Mace, G. M. 2010 Adaptation, plasticity and extinction in a changing environment: towards a predictive theory. *PLoS Biol.* **8**, e1000357. (doi:10.1371/journal.pbio.1000357)

Collen, B., Loh, J., Holbrook, S., McRae, L., Amin, R. & Baillie, J. E. M. 2009 Monitoring change in vertebrate abundance: the living planet index. *Conserv. Biol.* **23**, 317–327. (doi:10.1111/j.1523-1739.2008.01117.x)

Collen, B., McRae, Deinet, S., De Palma, A., Carranza, T., Cooper, N., Loh, J. & Baillie, J. E. M. In press. Predicting how populations decline to extinction. *Phil. Trans. R. Soc. B*.

Craigie, I. D., Baillie, J. E. M., Balmford, A., Carbone, C., Collen, B., Green, R. E. & Hutton, J. 2010 Large mammal population declines in Africa's protected areas. *Biol. Conserv.* **143**, 2221–2228. (doi:10.1016/j.biocon.2010.06.007)

Davies, T. J. *et al.* 2008 Phylogenetic trees and the future of mammalian biodiversity. *Proc. Natl Acad. Sci. USA* **105**, 11 556–11 563. (doi:10.1073/pnas.0801917105)

Diaz, S. & Cabido, M. 2001 Vive la difference: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.* **16**, 646–655. (doi:10.1016/S0169-5347(01)02283-2)

Díaz, S., Fargione, J., Chapin III, F. S. & Tilman, D. 2006 Biodiversity loss threatens human well-being. *PLoS Biol.* **4**, 1300–1305.

Diaz, S., Lavorel, S., de Bello, F., Quetier, F., Grigulis, K. & Robson, M. 2007 Incorporating plant functional diversity effects in ecosystem service assessments. *Proc. Natl Acad. Sci. USA* **104**, 20 684–20 689. (doi:10.1073/pnas.0704716104)

Dobson, A. *et al.* 2006 Habitat loss, trophic collapse, and the decline of ecosystem services. *Ecology* **87**, 1915–1924. (doi:10.1890/0012-9658(2006)87[1915:HLTCAT]2.0.CO;2)

Fewster, R. M., Buckland, S. T., Siriwardena, G. M., Baillie, S. R. & Wilson, J. D. 2000 Analysis of population trends for farmland birds using generalized additive models. *Ecology* **81**, 1970–1984. (doi:10.1890/0012-9658(2000)081[1970:AOPTFF]2.0.CO;2)

Fisher, D. O. & Owens, I. P. F. 2004 The comparative method in conservation biology. *Trends Ecol. Evol.* **19**, 391–398. (doi:10.1016/j.tree.2004.05.004)

Foden, W. *et al.* 2009 Species susceptibility to climate change impacts. In *Wildlife in a changing world—an analysis of the 2008 IUCN Red List of Threatened Species* (eds J.-C. Vié, C. Hilton-Taylor & S. N. Stuart), pp. 77–87. Gland, Switzerland: IUCN.

Food and Agricultural Organisation of the United Nations. 2001 *FAOSTAT–FAO statistical databases*. Rome, Italy: FAO.

Frankham, R. & Brook, B. W. 2004 The importance of time scale in conservation biology and ecology. *Ann. Zool. Fennici* **41**, 459–463.

Fuller, R. A., McDonald-Madden, E., Wilson, K. A., Carwardine, J., Grantham, H. S., Watson, J. E. M., Klein, C. J., Green, D. C. & Possingham, H. P. 2010 Replacing underperforming protected areas achieves better conservation outcomes. *Nature*, **466**, 365–367.(doi:10.1038/nature09180)

Gaston, K. J. & Fuller, R. A. 2008 Commonness, population depletion and conservation biology. *Trends Ecol. Evol.* **23**, 14–19. (doi:10.1016/j.tree.2007.11.001)

Gonzalez, A. & Loreau, M. 2009 The causes and consequences of compensatory dynamics in ecological communities. *Annu. Rev. Ecol. Evol. Syst.* **40**, 393–414. (doi:10.1146/annurev.ecolsys.39.110707.173349)

Green, R. E., Balmford, A., Crane, P. R., Mace, G. M., Reynolds, J. D. & Turner, R. K. 2005a A framework for improved monitoring of biodiversity: responses to the world summit on sustainable development. *Conserv. Biol.* **19**, 56–65. (doi:10.1111/j.1523-1739.2005.00289.x)

Green, R. E., Cornell, S. J., Scharlemann, J. P. W. & Balmford, A. 2005*b* Farming and the fate of wild nature. *Science* **307**, 550–555. (doi:10.1126/science.1106049)

Hawkins, B. A. 2001 Ecology's oldest pattern? *Trends Ecol. Evol.* **16**, 470. (doi:10.1016/S0169-5347(01)02197-8)

Inchausti, P. & Halley, J. 2001 Investigating long-term ecological variability using the global population dynamics database. *Science* **293**, 655–657. (doi:10.1126/science.293.5530.655)

Isaac, N. J. B. & Cowlishaw, G. 2004 How species respond to multiple extinction threats: evidence from primates. *Proc. R. Soc. Lond. B* **271**, 1135–1141. (doi:10.1098/rspb.2004.2724)

Jackson, S. T. & Sax, D. F. 2009 Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends Ecol. Evol.* **25**, 153–160. (doi:10.1016/j.tree.2009.10.001)

Jetz, W., Wilcove, D. S. & Dobson, A. P. 2007 Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biol.* **5**, 1211–1219. (doi:10.1371/journal.pbio.0050157)

Jones, K. E. *et al.* 2009 PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* **90**, 2648–2648. (doi:10.1890/08-1494.1)

Keith, D. A., Akçakaya, H. R., Thuiller, W., Midgley, G. F., Pearson, R. G., Phillips, S. J., Regan, H. M., Araujo, M. B. & Rebelo, T. G. 2008 Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biol. Lett.* **4**, 560–563. (doi:10.1098/rsbl.2008.0049)

Laurance, W. F. *et al.* 2006 Rapid decay of tree-community composition in Amazonian forest fragments. *Proc. Natl Acad. Sci. USA* **103**, 19 010–19 014. (doi:10.1073/pnas.0609048103)

Loh, J., Green, R. E., Ricketts, T., Lamoreux, J. F., Jenkins, M., Kapos, V. & Randers, J. 2005 The Living Planet Index: using species population time series to track trends in biodiversity. *Phil. Trans. R. Soc. B* **360**, 289–295. (doi:10.1098/rstb.2004.1584)

Mace, G. M. 2010 Drivers of biodiversity change. In *Trade-offs in conservation: deciding what to save* (eds N. Leader-Williams, W. M. Adams & R. J. Smith), pp. 349–364. New York, NY: Wiley-Backwell.

Mace, G. M. & Baillie, J. E. M. 2007 The 2010 biodiversity indicators: challenges for science and policy. *Conserv. Biol.* **21**, 1406–1413. (doi:10.1111/j.1523-1739.2007.00830.x)

Mace, G. M., Collar, N. J., Gaston, K. J., Hilton-Taylor, C., Akcakaya, H. R., Leader-Williams, N., Milner-Gulland, E. J. & Stuart, S. N. 2008 Quantification of extinction risk: IUCN's system for classifying threatened species. *Conserv. Biol.* **22**, 1424–1442. (doi:10.1111/j.1523-1739.2008.01044.x)

McKinney, M. L. & Lockwood, J. L. 1999 Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol. Evol.* **14**, 450–453. (doi:10.1016/S0169-5347(99)01679-1)

Millennium Ecosystem Assessment 2005 Ecosystems and human well-being: biodiversity synthesis. Washington, DC: World Resources Institute.

Naeem, S., Bunker, D., Hector, A., Loreau, M. & Perrings, C. (ed.) 2009 *Biodiversity, ecosystem functioning, and human wellbeing: an ecological and economic perspective.* Oxford, UK: Oxford University Press.

Owens, I. P. F. & Bennett, P. M. 2000 Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proc. Natl Acad. Sci. USA* **97**, 12 144–12 148. (doi:10.1073/pnas.200223397)

Pan-European Common Bird Monitoring Scheme (PECBMS). 2006 European common bird index:

population trends of European common birds 2005 update. Prague: European Bird Census Council. http://www.ebcc.info/pecbm.html

Parmesan, C. & Yohe, G. 2003 A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42. (doi:10.1038/nature01286)

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres Jr, F. 1998 Fishing down marine food webs. *Science* **279**, 860–863. (doi:10.1126/science.279.5352.860)

Petchey, O. L., McPhearson, P. T., Casey, T. M. & Morin, P. J. 1999 Environmental warming alters food-web structure and ecosystem function. *Nature* **402**, 69–72. (doi:10.1038/47023)

Pressey, R. L. 1994 Ad hoc reservations: forward or backward steps in developing representative reserve systems? *Conserv. Biol.* **8**, 662–668. (doi:10.1046/j.1523-1739.1994.08030662.x)

Price, S. A. & Gittleman, J. L. 2007 Bushmeat hunting, habitat loss and global extinction in the Artiodactyla. *Proc. R. Soc. B* **274**, 1845–1851. (doi:10.1098/rspb.2007.0505)

Purvis, A., Gittlemann, J. L., Cowlishaw, G. & Mace, G. M. 2000 Predicting extinction risk in declining species. *Proc. R. Soc. Lond. B* **267**, 1947–1952. (doi:10.1098/rspb.2000.1234)

R Development Core Team. 2006 *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing.

Sala, O. E. *et al.* 2000 Global biodiversity scenarios for the year 2100. *Science* **287**, 1770–1774. (doi:10.1126/science.287.5459.1770)

SCBD 2003 *Handbook of the convention on biological diversity.* London, UK: Earthscan.

Scholes, R. J. & Biggs, R. 2005 A biodiversity intactness index. *Nature* **434**, 45–49. (doi:10.1038/nature03289)

Sekercioglu, C. H., Daily, G. C. & Ehrlich, P. R. 2004 Ecosystem consequences of bird declines. *Proc. Natl Acad. Sci. USA* **101**, 18 042–18 047. (doi:10.1073/pnas.0408049101)

Sibly, R. M., Barker, D., Hone, J. & Pagel, M. 2007 On the stability of populations of mammals, birds, fish and insects. *Ecol. Lett.* **10**, 970–976. (doi:10.1111/j.1461-0248.2007.01092.x)

Telfer, M. G., Preston, C. D. & Rothery, P. 2002 A general method for measuring relative change in range size from biological atlas data. *Biol. Conserv.* **107**, 99–109. (doi:10.1016/S0006-3207(02)00050-2)

Tilman, D., May, R. M., Lehman, C. L. & Nowak, M. A. 1994 Habitat destruction and the extinction debt. *Nature* **371**, 65–66. (doi:10.1038/371065a0)

Vellend, M., Verheyen, K., Jacquemyn, H., Kolb, A., Van Calster, H., Peterken, G. & Hermy, M. 2006 Extinction debt of forest plants persists for more than a century following habitat fragmentation. *Ecology* **87**, 542–548. (doi:10.1890/05-1182)

Vie, J.-C., Hilton-Taylor, C. & Stuart, S. N. 2009 Wildlife in a changing world: an analysis of the 2008 Red List of Threatened Species. pp. 180. Gland, Switzerland: IUCN.

Visconti, P., Pressey, R. L., Segan, D. B. & Wintle, B. A. 2010 Conservation planning with dynamic threats: the role of spatial design and priority setting for species' persistence. *Biol. Conserv.* **143**, 756–767. (doi:10.1016/j.biocon.2009.12.018)

Wood, S. N. 2006 Generalized additive models: an introduction with R. In *Texts in statistical science.* Boca Raton, USA: Chapman & Hall/CRC.

Yamaura, Y., Amano, T., Koizumi, T., Mitsuda, Y., Taki, H. & Okabe, K. 2009 Does land-use change affect biodiversity dynamics at a macroecological scale? A case study of birds over the past 20 years in Japan. *Anim. Conserv.* **12**, 110–119. (doi:10.1111/j.1469-1795.2008.00227.x)