

LETTER

Minimum viable population sizes and global extinction risk are unrelated

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Abstract

Theoretical and empirical work has shown that once reduced in size and geographical range, species face a considerably elevated risk of extinction. We predict minimum viable population sizes (MVP) for 1198 species based on long-term time-series data and model-averaged population dynamics simulations. The median MVP estimate was 1377 individuals (90% probability of persistence over 100 years) but the overall distribution was wide and strongly positively skewed. Factors commonly cited as correlating with extinction risk failed to predict MVP but were able to predict successfully the probability of World Conservation Union Listing. MVPs were most strongly related to local environmental variation rather than a species' intrinsic ecological and life history attributes. Further, the large variation in MVP across species is unrelated to (or at least dwarfed by) the anthropogenic threats that drive the global biodiversity crisis by causing once-abundant species to decline.

Keywords

Density dependence, extinction correlates, generalized linear mixed models, minimum viable population size, model-averaging, population variability.

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INTRODUCTION

With the emergence of conservation biology as a distinct discipline in the late 1970s came a need to characterize quantitatively the long-term viability of small populations at risk of imminent extinction (Soulé & Wilcox 1980). It was recognized that given the limited resources available for biodiversity management (especially in developing countries) and the ever-increasing conflict between humans and wildlife, the efficient application of extinction theory for applied conservation was (and still is) desperately required (Shaffer 1981; Gilpin & Soulé 1986). Theoretical and empirical work has repeatedly shown that once reduced in size and geographical range, populations face a considerably elevated risk of extinction (MacArthur & Wilson 1967; Terborgh & Winter 1980), and a scientific expression of this phenomenon is the concept of the 'minimum viable population' (MVP). An MVP is defined as the number of individuals required to have a specified probability of persistence over a given period of time (Shaffer 1981; Gilpin & Soulé 1986; Nunney & Campbell 1993). Theoretical expectations for MVP vary from 50 to 10 000 individuals

based on the postulated effects of demographical, genetical and environmental variation (Reed *et al.* 2003), with the limited available empirical evidence pointing to the upper end of this range (Newmark 1987; Berger 1990; Thomas 1990; Harcourt 2002). However, present estimates of MVP are at best highly uncertain, difficult to generalize, and give little idea of the variance observed among taxa (Shaffer 1987; Reed *et al.* 2003).

Over the past few decades, conservation biologists have regularly used models to estimate MVPs for imperiled species, often at considerable expense and with substantial data requirements (Boyce 1992; Nunney & Campbell 1993; Reed *et al.* 2003), despite the MVP concept falling out of favour with some authors (e.g. Reed *et al.* 2002). Procedures such as gap analysis, reserve selection algorithms and some of the World Conservation Union's (IUCN) Red List criteria are also underpinned by the notion that species with small and range-restricted populations are particularly extinction prone (Prendergast *et al.* 1999; Brook *et al.* 2002). For example, IUCN Criterion D rates the level of threat faced by a species based on a set of threshold absolute population sizes, whilst Criterion E concerns the projected risk of

extinction faced by a species over specified time periods (IUCN 2005). That said, the defining feature of MVP is that the risk of extinction is fixed, and the question of how large a population must be to avoid this risk is asked. In contrast, population viability analysis and the threat categories of IUCN (endangered, vulnerable, lower risk, etc.) provide an assessment of a species' probability of extinction given its current population size and structure and the totality of threatening processes it faces.

Political, administrative and management decisions made for threatened species are frequently performed so without the benefit of complete information and are often subject to severe budgetary constraints, underscoring the need to develop robust generalizations (Belovsky *et al.* 2004) for MVP. Moreover, it is reasonable to expect that MVPs should be correlated with basic life history traits or other ecological attributes (see Composite predictors), given that other measures of a species' resilience (e.g. IUCN Red Listing, the taxonomic distribution of local extinctions following a disturbance, extinctions in geological time) are indeed amenable to such generalizations (McKinney 1997; Purvis *et al.* 2000a,b; Blackburn & Duncan 2001; Kotiaho *et al.* 2005). Alternatively, if the fate of small populations is largely independent of the processes that ultimately caused species to become endangered, seeking a broad-scale correlative framework for MVP may be quixotic.

Here, we use a set of high-quality, long-term population abundance time-series data to estimate MVPs for 1198 species spanning a wide range of taxa, habitats and life histories. We then address the question of whether there are common processes explaining the observed distribution of MVPs, and whether surrogate predictors can be used to infer MVPs when detailed demographical or time-series data are unreliable or unavailable. We report a striking lack of predictability in MVP, with essentially no association to ecology, life history or human threat. This absence of any clear pattern is in stark contrast to strong relationships between global risk of decline (as assigned by the IUCN) and these same ecological and life-history attributes. This important (albeit negative) result reinforces the spatial disconnection between the type of conservation intervention required to manage the local risks faced by small imperiled populations and the approaches needed to arrest global declines (which can be underpinned by some useful generalizations).

METHODS

Time-series data

Population dynamics time-series data were obtained primarily from the Global Population Dynamics Database (GPDD), which provides time-series data for nearly 5000

populations spanning over 1400 species. Other sources obtained from peer-reviewed and grey literature (including online material) were used where the data were either of superior quality to, or were unavailable from the GPDD. Unlike previous applications of GPDD data, we developed a strict and extremely comprehensive set of filtering criteria to remove the many ambiguities and inconsistencies therein (details in Appendix S1). This produced a reduced and coherent database suitable for cross-species meta-analysis. Key issues requiring resolution included biases due to over-representation of some species (multiple time series), composite (multiple species) data, taxonomically unresolved units, uneven sampling frequencies, different durations, missing values, quality and method of representation (e.g. direct censuses vs. indirect harvest indices) and different data transformations. Our objective standardization protocol resulted in a single time series for each species that ensured a minimum quality and adequate duration (> 8 observed time-step transitions) for reliable model fitting (Morris & Doak 2002). The final dataset of 1198 species (629 invertebrates, 529 vertebrates, 30 plants) had a mean duration of 22 year-to-year transitions, mean rate of population increase (r) = 0.005 (σ_r^2 = 0.733), and a coefficient of variation in population size = 0.610 (see Table S1).

Population models

Previous model-based estimates of MVP have generally ignored model-selection uncertainty and chosen a single 'best' model (which is often arbitrary and overly complex given the available data), although it is widely acknowledged that there is no single population dynamical framework that can be applied to all taxa (Turchin 2003). We adopted a multiple-working hypotheses approach based on information-theoretic model selection and multimodel inference (Burnham & Anderson 2002) and used an *a priori* model-building strategy to arrive at a set of five population dynamics models commonly used to describe phenomenological time-series abundance data (Sæther *et al.* 2002; Turchin 2003; Fryxell *et al.* 2005). These encompassed directional and non-directional density-independent growth and different forms of density regulation based on variants of the generalized θ -logistic population growth model:

$$\log\left(\frac{N_{t+1}}{N_t}\right) = r = r_m \left[1 - \left(\frac{N_t}{N_a}\right)^\theta\right] + \varepsilon_t$$

where N_t , population size at time t ; r , realized population growth rate; r_m , intrinsic population growth rate; N_a , the population size when $r = 0$ and θ (when fitted) permits a nonlinear relationship between rate of increase and abundance. The term ε_t has a mean of zero and a variance (σ^2)

that reflects environmental variability in r . Model variants used were (i) random walk (RW; $r_m = 0, \sigma$); (ii) exponential (EX) growth ($r_m, \theta = -\infty, \sigma$); (iii) Ricker-logistic (RL) growth ($r_m, N_a, \theta = 1, \sigma$); (iv) Gompertz-logistic (GL) growth ($r_m, \log_e[N_a], \theta = 1, \sigma$, fitted to $\log_e[N_a]$); and (v) θ -logistic (TL) growth (r_m, N_a, θ, σ). For each species, we used maximum-likelihood estimation to fit model parameters (via linear regression for RW, EX, RL and GL, and nonlinear regression using Newton optimization for TL) and Kullback–Leibler information to assign relative strengths of evidence (AIC_c weights) to each model (Burnham & Anderson 2002). For each fitted model, we used a numerical simulation optimization routine (> 100 000 iterations per species) to estimate two MVPs by varying initial size until the species had (i) 0.99 probability of persisting 40 generations (GMVP) and (ii) 0.90 probability of persisting 100 years (YMVP). GMVP was preferred because apparently contrasting demographics among large- and small-bodied taxa may become negligible when scaled by generation length (Sinclair 1996; Frankham & Brook 2004).

Composite predictors

To determine whether there are common processes influencing a species' MVP and if surrogate predictors of 'extinction risk' can be used to estimate MVP when detailed demographical or time-series data are unavailable, we undertook an extensive review of the available literature to determine which ecological and anthropogenic variables have been shown or postulated to increase a species' vulnerability to extinction (e.g. Gilpin & Soulé 1986; WCMC 1992; McKinney 1997; Purvis *et al.* 2000a,b; Blackburn & Duncan 2001; IUCN 2005; Kotiaho *et al.* 2005). We compiled nineteen variables encompassing morphological, life-history, ecological and behavioural attributes and measures of human impact that have been cited in the literature, and then reduced this number of predictors based on theory and logic to six derived (composite) predictors: (i) Threat Index (TI) – a binary index indicating whether a population or species was considered to be of conservation concern, (ii) Geographic Range (RA) – distribution of the species expressed as a continuous variable (0–1) derived from five categories (global, single phytogeographical or oceanic region, single biome, narrow endemic < 500 km², very narrow endemic < 50 km²), (iii) Human Impact (HI) – a measure encapsulating the extent of range or habitat loss, and the severity of direct (culling, etc.) or indirect population suppression (e.g. pollution, competition with weeds), (iv) Body Size (BS) – an allometric scaling covariate, (v) Ecological Flexibility (EF) – a logical composite of dispersal ability, trophic level and the extent of ecological specialization, and (vi) Demographics (DE) – encapsulating the repro-

ductive life history of species (i.e. age at sexual maturity, fertility, reproductive strategy and longevity). The logic and justification, derivation and associated assumptions for these correlates are described fully in Appendix S1 and Tables S2 and S3 – space constraints prohibit the presentation of this detailed information in the printed paper.

One might argue that variables predicted *a priori* to explain variation in extinction risk might not be expected to correlate with MVP, given the latter does not encapsulate the risks imposed by deterministic drivers. This is because the calculation of MVPs requires setting an acceptable level of risk and using knowledge of the population's intrinsic dynamics and stochastic influences to calculate an extinction – 'proof' population size in the absence of deterministic pressures. Although our composite predictors do indeed recapitulate deterministic stressors, they also describe drivers of intrinsic population dynamics and stochastic processes. *Threat Index* and *Human Impact* reflect strong deterministic impacts, but also indicate the potential for increasing environmental variation via such processes as habitat fragmentation (Fahrig 2001; IUCN 2005). *Wide-ranging* species may be buffered against environmental fluctuations (Purvis *et al.* 2000a) because (for instance) only certain subpopulations would succumb to localized catastrophes (e.g. fire, severe weather). *Body Size* is strong predictor of intrinsic dynamics such as density-dependent regulation and maximum rates of population growth (McKinney 1997), whilst *Demographics* describes variation in life-history strategies that evolve to suit particular environmental circumstances (Frankham & Brook 2004). Finally, *Ecological Flexibility* should indicate how sensitive a species will be to stochastic events influencing demographic rates such as survival and fecundity (Gilpin & Soulé 1986).

Statistical analyses

To examine the relative importance of each derived ecological variable to predict MVP, we used a form of model averaging based on all-subsets selection of generalized linear mixed-effects models (GLMM). All GLMMs were fitted to log model-averaged MVPs using a quasi-Poisson error distribution with an identity link function in the *R* statistical package v2.0.1 (Ihaka & Gentleman 1996). The random effects error structure of GLMM corrects for non-independence of statistical units (species) due to shared evolutionary history (Felsenstein 1985), and permits the 'random effects' variance explained at different levels of hierarchical clustering (Class/Order/Family) to be decomposed (Blackburn & Duncan 2001). The six derived predictor variables were modelled as 'fixed effects'. Interactions terms were not included because our possible model set was already large and the rational

interpretation of interaction trade-offs for composite predictors is problematical.

In addition to the combined species model using all correlates, we undertook separate analyses to evaluate the sensitivity of our results to taxonomic representation, size of MVP estimates, extent of geographical range and length of monitoring (reported in Results) and treatment of incomplete data or uncertain risk classifications for the TI correlate (reported in the online Appendix S1). We also considered an alternative 'mixed' definition for MVP as a 0.90 probability of persisting the longer of 100 years or 40 generations, but in this instance only fitted the global (saturated) correlates model.

To provide an independent check of the biological value of the derived ecological predictors with respect to a measure of extinction proneness, we also constructed analogous models using the IUCN Red Listing (IUCN 2005) for the vertebrates (none of the invertebrates in our database were on the IUCN Red List). These models were fitted (after removing TI as a predictor) using a binomial error distribution and logit link function. Of the 529 vertebrates, 70 were Red Listed (anything other than *Least Concern*, excluding *Data Deficient* and *Not Evaluated*).

In the case of a large number of closely related models, the designation of any single best model is inappropriate because selection varies from dataset to dataset even if they are generated by the same underlying processes. Instead, inference based on all possible models eliminates model-selection bias and provides a balanced, relative measure of each predictor's importance. In the case of six predictors, there are $2^6 = 64$ possible models in an all-subsets selection ($2^5 = 32$ models using IUCN listing as the response), which is a considerable improvement over the $2^{19} = 524\,288$ possible models based on the original correlates postulated prior to derivation of the six *a priori* composite predictors. Model averaging was based on Akaike's Information Criterion corrected for small samples (AIC_c). The weights of evidence (w_{+i}) for each predictor were calculated by summing the model AIC_c weights (w_i) over all models in which each term appeared. However, the w_{+i} values are relative, not absolute because they will be > 0 even if the predictor has no contextual explanatory importance (Burnham & Anderson 2002). To judge which predictors are relevant to the data at hand, a baseline for comparing relative w_{+i} across predictors is required. We randomized the data for each predictor separately within the dataset, re-calculated w_{+i} , and repeated this procedure 100 times for each predictor. The median of this new randomized w_{+i} distribution for each predictor was taken as the baseline (null) value (w_{+0}). For each term the absolute weight of evidence (Δw_{+i}) was obtained by subtracting w_{+0} from w_{+i} . Predictors with Δw_{+i} of zero or less have essentially no explanatory power.

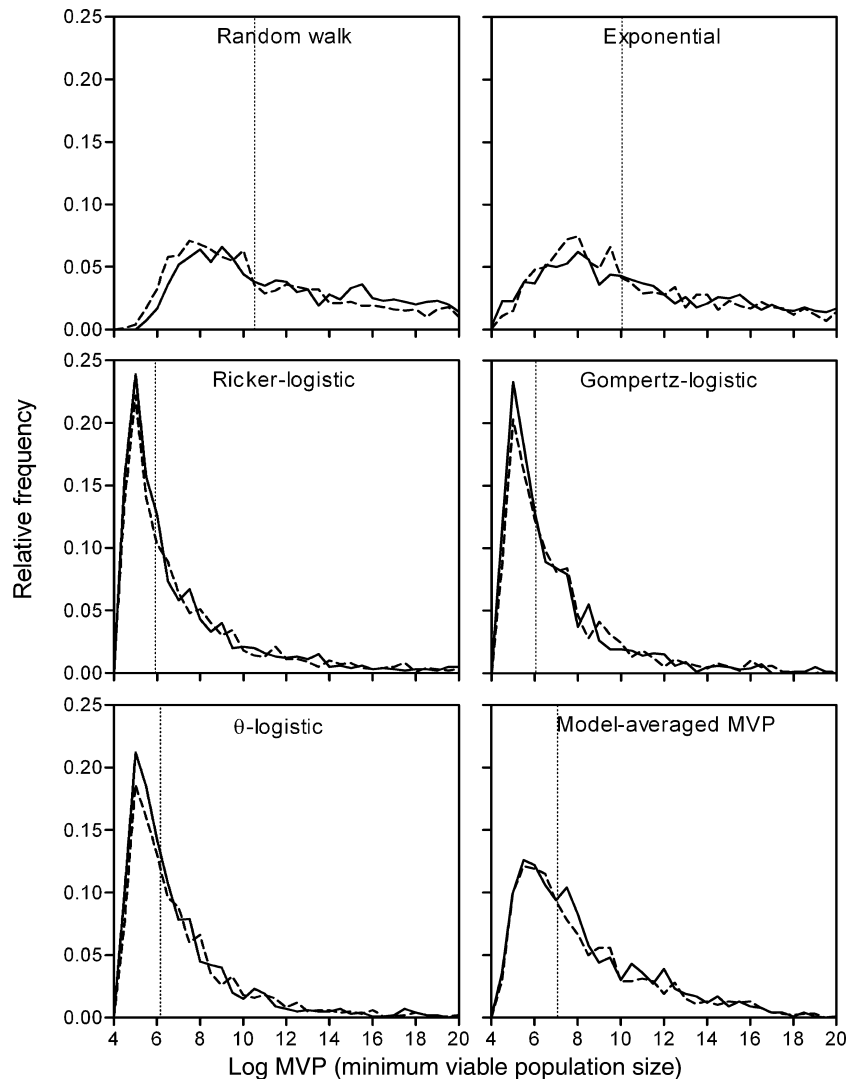
RESULTS AND DISCUSSION

Minimum viable population size estimates

The generational MVPs (median estimates across 1198 species) were similar for the three density-dependent models ($GMVP_{RL} = 376$, $GMVP_{GL} = 431$, $GMVP_{TL} = 484$), whereas the density-independent model estimates were nearly two orders of magnitude larger ($GMVP_{RW} = 37\,304$, $GMVP_{EX} = 23\,315$, Fig. 1 – dashed lines). The MVPs estimated on a yearly time scale demonstrated similar trends ($YMVP_{RL} = 335$, $YMVP_{GL} = 372$, $YMVP_{TL} = 391$, $YMVP_{RW} = 250\,216$, $YMVP_{EX} = 98\,997$, Fig. 1 – solid lines). For all species combined, the relative strength of evidence (standardized average AIC_c weight) for each of the five models was 0.226 (RW), 0.078 (EX), 0.230 (RL), 0.385 (GL) and 0.080 (TL). The most-probable reason for the difference in estimated MVP across different models is that density-dependent variants encapsulate population dynamics constrained to fluctuate around an equilibrium N . Thus, density-dependent models provide greater long-term stability than the density-independent models, which lack endogenous control and are hence more prone to the vagaries of environmentally induced fluctuations (Turchin 2003). The trends in MVP and model weights were consistent across all major taxonomic groups. For each species, the MVP predicted by a given model was multiplied by its AIC_c weight for that species' time series. A model-averaged estimate of MVP for each species was calculated by summing these products across all five models (Fig. 1 – bottom right panel).

Of the 529 vertebrate species' time series, 83 represented relatively high-precision, direct-count data and the remainder were based on indirect indices of abundance (e.g. catch per unit effort). To test the impact on MVP of potential observation or measurement errors in estimating abundance, we re-calculated the geometric mean model-averaged GMVP for the direct- vs. indirect-count categories. The 83 direct-count species resulted in a median GMVP of 933 (633–2724; 95% bootstrapped confidence intervals based on 10 000 iterations), and for the remaining species, median GMVP = 2943 (2149–4077, 95% CI). We also evaluated the sensitivity of our results to the 207 species' time series (covering all taxa), which contained at least one non-terminal observation of zero abundance (see Appendix S1 for details). Zeros may indicate low detectability of individuals and hence a higher observation error in the population index. For the time series with zero abundance counts, GMVP was 5310 (3030–8017, 95% CI) compared with just 938 (774–1095, 95% CI) for the remaining 991 species, although the fit of the correlates model (see Correlates of MVP) was poor in both instances. On the basis of these two sensitivity analyses, we conclude that measurement or observation

Figure 1 Frequency distribution of log minimum viable population (MVP) sizes for five population dynamics models across 1198 species. MVP estimates were based on two different persistence criteria: (i) population size resulting in a > 99% probability of persistence over 40 generations (dashed line) and (ii) > 90% probability of persistence over 100 years (solid line). Random walk and exponential models are density-independent, whereas the Ricker-, Gompertz- and θ -logistic are density-dependent. The model-averaged log_e MVP distribution (based on AIC_c weights of the five listed models) is also shown. Median values for each model under MVP criterion (i) are indicated with a vertical dotted line.



error inflates apparent variation in population dynamics and hence causes MVP to be overestimated (i.e. providing a more-precautionary estimate of minimum viable population sizes).

Correlates of MVP

The set of composite predictors of extinction risk failed to explain the cross-species differences we observed in MVP. The GLMM using GMVP and YMVP as response variables explained an extremely small component of the variation (% deviance explained, %DE) in the data (%DE[GMVP] = 0.24%, %DE[YMVP] = 2.1%). When all six derived predictors were fitted to each of the five model predictions independently, the highest %DE[GMVP] was for the RW model (1.78%), and the EX model for %DE[YMVP]

(7.1%). Thus the model-averaging procedure reduced overall deviance explained (because it accounted explicitly for model-selection uncertainty), but not substantially so. Length of monitoring data can affect population dynamics predictions (Fieberg & Ellner 2000) and indeed influenced the fit of the saturated model – the deviance explained for time series of < 15 transitions ($n = 242$) was 1.1%, compared with 9.4% for a the fit to time series of > 40 transitions ($n = 103$). However, the difference in the geometric mean model-averaged GMVP was particularly striking: for the short time series, it was 11 860 (7260–23 039, 95% CI) vs. 1108 (631–2706, 95% CI) for the long time series. The median strength of evidence (AIC_c weight, range 0–1) for the density-dependent models was 0.424 and 0.924 for the short- and long-time series respectively. This difference in support for endogenous regulation is the

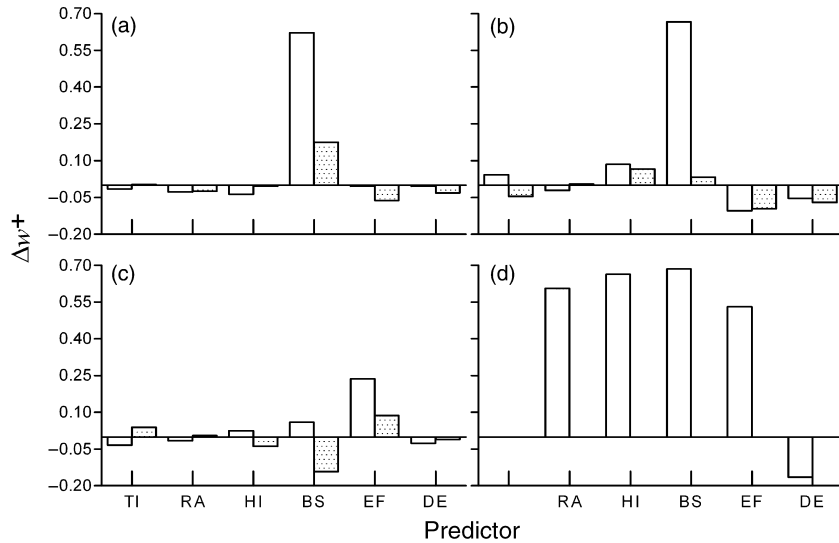


Figure 2 Absolute weights of evidence (Δw^+) of six derived predictors [threat index (TI), geographical range (RA), human impact (HI), body size (BS), ecological flexibility (EF) and demographics (DE)] for explaining variation in \log_e MVP (averaged across five models) based on two different persistence criteria: population size resulting in a > 99% probability of persistence over 40 generations (shaded bars) and > 90% probability of persistence over 100 years (clear bars). (a) Δw^+ shown for all species combined, (b) for vertebrates only and (c) for invertebrates only. Δw^+ are also shown for models where IUCN threatened status (Red Listed or not) was the response variable (d). Predictor Δw^+ were calculated using model averaging over all possible generalized linear models containing those predictors. Predictors with weighting of zero or less have essentially no explanatory power.

most-likely driver of the lower predicted MVPs for the long time series group.

For all species combined, body size was the only important predictor of YMVP, but its importance was reduced for GMVP (Fig. 2a). Figure 2b hints of an allometric scaling of MVP for the vertebrates, but body size was irrelevant for the invertebrates (Fig. 2c). Detecting an 'important' predictor here, even with low %DE, reflects in part the statistical power of the large dataset. Examining the results for vertebrates (Fig. 2b) and invertebrates (Fig. 2c) separately, the body-size effect disappears for GMVP, suggesting the large average difference in body size between these two phyla drives the relationship observed for all species combined. Ecological flexibility demonstrated some importance for invertebrates (Fig. 2c). Fitting the saturated model to specific taxa did not greatly improve the %DE[GMVP]: 2.1% for birds ($n = 225$), 8.9% for mammals ($n = 152$), 1.0% for fish ($n = 115$), and 0.11% for insects ($n = 603$), nor when only species with small (GMVP < 5000 individuals: 8.4%DE, $n = 787$) or large (GMVP > 20 000 individuals: 2.3%DE, $n = 277$) MVPs were considered. Similarly, the model fit remained poor when we examined only those species restricted to a single phytogeographical region or less (0.61%DE, $n = 777$) or alternatively those with continental/global distributions (0.43%DE, $n = 421$); range was not included as a predictor variable in this

instance. Use of the alternative mixed definition of GMVP (0.90 probability of persisting the longer of 100 years or 40 generations) increased the overall GMVP estimate slightly to 1414 (1169–1700, 95% CI) but did not noticeably improve the fit of the correlates model (0.65%DE, $n = 1198$).

The general low power of the derived composite predictors to explain variation in MVP, irrespective of the group being examined, might indicate that they are not robust variables associated with extinction risk. However, GLMMs using IUCN Red Listing as the dependent variable (listed or not) showed that all derived predictors (except Demographics) were extremely useful in explaining anthropogenic threat status (%DE[IUCN] = 51.6%, Fig. 2d). Some have argued that IUCN listing is a poor indicator of a species' threat status (Webb & Carrillo 2000) given that it relies on crude surrogates of risk and often sparse data, whilst others have demonstrated the Red List's utility for broadly predicting extinction risk (Keith *et al.* 2004; Bucharth *et al.* 2005). The strong correlation between the probability of IUCN listing and our composite ecological predictors underscores the real-world applicability of our correlates. This verification is a key component of our argument because it demonstrates that the lack of correlation between MVP and our chosen ecological predictors is authentic and not simply a result of poorly formulated explanatory terms.

MVP and threatened species

Do species with low MVP tend to be less at risk according to IUCN classification? Those vertebrate species in the database that were not IUCN Red Listed had a median GMVP of 2394 (1833–3288; 95% CI), whereas the 70 threatened species had a median GMVP of 4885 (1319–12 149; 95% CI). Therefore, threatened species may have higher MVPs than their non-threatened counterparts, but this difference could not be distinguished statistically because of the wide and overlapping confidence limits. Further, there was no sequential pattern of increasing GMVPs with higher risk classification (all CIs from *Critically Endangered* through to *Lower Risk: Conservation Dependent* had overlapping limits).

Ecological predictors of threatened status (e.g. IUCN Red List categorization) signify a species' sensitivity to the ultimate causes of extinction (e.g. direct or indirect human impacts; McKinney 1997; Purvis *et al.* 2000b), whereas MVPs reflect the stochastic hazards encountered by populations that have already been reduced in size (Shaffer 1981; Gilpin & Soulé 1986). The size required for long-term viability in the face of stochastic variation will depend largely on a host of population-specific factors such as the magnitude and frequency of fluctuations in the environment and the population's response to these (Lande 1993), the degree of inter-specific competition (Gilpin & Soulé 1986), metapopulation dynamics (Hanski *et al.* 1996) and the importance of population regulation (Sæther *et al.* 2002; Turchin 2003). On the basis of our results, these influences do not appear to be amenable to generalization at spatial scales larger than the local population.

What then, determines the relative viability of small populations for different species given the clear lack of support for ecological and anthropogenic threats affecting MVP? It is axiomatic that long-term persistence is foreclosed (and therefore the question of MVP becomes irrelevant) if a population continues to decline due to external deterministic drivers (e.g. habitat loss, over-exploitation; Caughley 1994). Thus, MVPs appear to be driven primarily by the stochastic hazards faced by small populations that are not (or at least no longer) declining deterministically, with their extinction risk being largely a function of demographic and environmental variance and population size (Lande 1993). A GLMM using only a population's intrinsic growth rate and its variance (r_m , V_e) showed for our dataset that the model-averaged estimates of r_m and V_e explain 49.8% of the deviance observed in GMVP (c.f. %DE[GMVP] = 0.4% for the ecological/anthropogenic predictors). When modelled in isolation, %DE[V_e] = 42.4% and %DE[r_m] = 6.0%, but the two-predictor model was the most parsimonious (c. 100% of the AIC_c weight).

Are the MVP estimates we present sufficiently robust to be used by conservation managers to set recovery targets for threatened species or determine whether habitat reserves cover areas of sufficient size to maintain viable populations? Our results clearly have heuristic value (Brook *et al.* 2002) and the multimodel inferential methods we used to interrogate the time series are statistically sound. However, deciding on the biological validity of the absolute numbers is complex for at least three reasons: (i) our analysis of direct- vs. indirect-count data implies that observation or measurement error in abundance estimates inflates predicted MVP; (ii) unmeasured external processes may have suppressed population growth rates in the historical time series; and conversely (iii) our relatively simple phenomenological models do not include demographical stochasticity, fluctuations associated with an unstable stage structure, nor the negative and cumulative genetic problems associated with small population sizes; these omissions probably cause an underestimation of MVP. On balance, we argue that although these MVPs provide a useful rule of thumb for species conservation, they should not be used as precise conservation targets.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available online for this article from <http://www.Blackwell-Synergy.com>:

Appendix S1 Data sourcing/filtering methods and derivation of the correlates.

Table S1 Summary statistics (averages across groups, by taxon) of the population dynamics time-series data set of 1198 species.

Table S2 Examples of the composite predictors and correlates scores assigned to three vertebrate and two invertebrate species.

Table S3 Excel database listing all species-specific MVPs and correlates.

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