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Predictability of ecological and evolutionary dynamics in a changing world

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Ecological and evolutionary predictions are being increasingly employed to inform decision-makers confronted with intensifying pressures on biodiversity. For these efforts to effectively guide conservation actions, knowing the limit of predictability is pivotal. In this study, we provide realistic expectations for the enterprise of predicting changes in ecological and evolutionary observations through time. We begin with an intuitive explanation of predictability (the extent to which predictions are possible) employing an easy-to-use metric, predictive power $PP(t)$. To illustrate the challenge of forecasting, we then show that among insects, birds, fishes and mammals, (i) 50% of the populations are predictable at most 1 year in advance and (ii) the median 1-year-ahead predictive power corresponds to a prediction R^2 of only 20%. Predictability is not an immutable property of ecological systems. For example, different harvesting strategies can impact the predictability of exploited populations to varying degrees. Moreover, incorporating explanatory variables, accounting for time trends and considering multivariate time series can enhance predictability. To effectively address the challenge of biodiversity loss, researchers and practitioners must be aware of the information within the available data that can be used for prediction and explore efficient ways to leverage this knowledge for environmental stewardship.

1. Introduction

Three decades ago, Jared Diamond [1] and Edward O. Wilson [2] summarized the main human-caused stressors to biodiversity as habitat degradation, fragmentation and loss, overexploitation, introduction of non-native species and diseases and pollution. Not only do these threats continue to impact life on Earth, they are joined by global warming, which is accelerating the decline of biodiversity worldwide [3,4]. Worryingly, these stressors combine synergistically to form a perfect storm [5], and their impacts can percolate via cascading effects through entire ecosystems: biodiversity loss may be regarded as a harbinger of ecosystem collapse [6]. In addition to threatening population persistence and species richness, human stressors are potent agents of rapid evolutionary change in the wild, with exploitation leading the other stressors in driving phenotypic changes in populations [7,8]. Thus, we are experiencing not only loss of species but also loss of variation within species, with both of these types of losses changing life on Earth (e.g. [9–11]).

Our understanding of the mechanisms underlying stressor effects and the global extent of these effects on biodiversity has improved (e.g. [12–14]), and collections of long-term data allow testing hypotheses about changes in wildlife populations (e.g. [15] and references therein). Global synoptic indicators of biodiversity change include the Red List Index [16] and the Living Planet Index [17]. These indicators are invaluable to inform—and

ideally prompt actions by—governments and the general public. Several authors have nonetheless bemoaned conservation biology and restoration ecology as generally lacking substantial efforts to model and predict future changes to guide mitigation actions (e.g. [18–20]). The reasons are multifaceted, and mechanistically predicting biodiversity responses to current and predicted future stressor levels continues to be a formidable task (e.g. [21], but see [22]). Yet, Bodner *et al*. [23, p. 10] aptly note that 'as researchers, we are often acutely aware of how much we do not know and therefore get stuck at "more research is required". However, environmental changes are increasingly affecting our world, and decisions are made whether or not we are involved'.

Compared with the ecological dimensions of biodiversity loss, our understanding of genetic diversity loss is less developed [12,24]. This is unfortunate because genetic variation is the raw material enabling species to robustly adapt to a changing world [24]. Despite the growing recognition of this dimension of biodiversity, predictions in evolutionary science face many challenges similar to ecology [25–27]. Evolutionary changes depend on changes in the genetic make-up of populations over time, but long-term genetic datasets continue to be rare. Therefore, analyses are often performed on phenotypic changes in the wild, which are routinely measured [13]. Phenotypic changes, however, do not necessarily imply genetic changes; instead, they could be the result of phenotypic plasticity. Nonetheless, phenotypic changes in larger populations, for species with shorter generation times, or in response to harsher environmental conditions are more likely to represent genetic changes [13].

How well can future population changes in abundance or phenotype be predicted? And is it fundamentally possible to predict future states of biodiversity [28]? Answers to the first question often centre around forecast accuracy (e.g. [29]), that is, how good a model has to be to make good predictions. Unfortunately, even a very good model can fail to make useful predictions about inherently unpredictable events. For example, assuming heads and tails have equal probability is an excellent statistical model for flipping a coin, but this is not much help in predicting the outcome of the next flip. Therefore, instead of focusing on how well models fit data, we address the second question, asking how much information is contained in a dataset to make predictions and how a lack of information creates a barrier to prediction dictated by a predictability limit of the system [28–32]. Here, we follow the definition that 'predictability is the study of the extent to which predictions are possible' [31, p. 2425]. While the issue of an inherent limit of predictability has been studied for several decades in different fields, chief among them climatology [33], ecologists and evolutionary biologists have only recently started tackling it [25,26,28,29,34].

Our goal is to argue that biodiversity conservation needs to adopt the concept of predictability to better design strategies and policies to constrain human-caused threats to life on Earth. After an intuitive presentation of the concept of predictability, we apply it to approximately 1600 population abundance and phenotype time series of invertebrate and vertebrate species to ask about the limit to predictability of ecological and evolutionary systems. We then discuss predictability addressing the following two central topics in biodiversity conservation: managed (exploited) populations and environmental forcing (explanatory variables) that affects the dynamics of population abundance and phenotypic traits. Our examples show that predictability is not an immutable property of species but instead can be influenced by management strategies and environmental changes. Furthermore, we offer statistical evidence and theoretical proof for several previously stated but unresolved hypotheses ([29,35] and references therein). We conclude by summarizing why adopting the concept of predictability in biodiversity conservation will improve our strategies to counteract human-caused stressors of wildlife populations.

2. Methods

Instead of an exhaustive technical description of predictability (e.g. [29–31]), we introduce the concept using an illustrative ecological example, the population of wolves on Isle Royale (MI, USA). We focus on the period 1959–2011 when the population experienced large fluctuations, but before it started a precipitous decline [36] (figure 1 and electronic supplementary material, appendix 2). We use this dataset for two related analyses. We start by focusing on the wolf data alone to introduce the main ideas and elements of predictability (figure 1*a*). Second, we include covariate data to demonstrate how it may increase predictability (figure 1*b*). For the second analysis, we consider (i) the wolves' main prey (moose; given the available data, we analyse senescent moose) and (ii) the short- and long-term effects of a canine parvovirus outbreak (figure 1*b*). Additional methodological details and information on the covariates can be found in electronic supplementary material, appendix 2.

Many textbook deterministic models show how density-regulated populations eventually reach a 'carrying capacity'. The stochastic analogue is the stationary distribution, with a mean (the 'carrying capacity') and a variance capturing, for example, yearly fluctuations in abundance around the mean (figure 1*a*). A density-regulated population in the long term will settle on an average size (the mean of the stationary distribution) and fluctuate around this mean according to the variance and higher statistical moments of the stationary distribution. If the properties of a stochastic process do not change over time, the stationary distribution offers the simplest way of forecasting future abundances: just predict that the mean and uncertainty in the abundance of a species in any future year are given by the stationary distribution, regardless of the current abundance. This approach is easy to implement because the estimated sample mean, variance and other moments of the time series suffice to characterize the stationary distribution. A different but equally simple approach is to assume that next year's abundance will be equal to the current one. This assumption implies there is no density dependence regulating the population, but instead, the population fluctuates by a random walk. Both of these approaches, however, are unlikely to be very accurate. Predictability, in a nutshell, takes a position between these two extremes: predictability is based on the amount of information in a time series that can be used to project a population's transition from the current state to the stationary distribution.

When conditioning forecasts on current abundance, the forecast dynamics are characterized by the transition distribution, with mean and variance (also called forecast error variance [30]) that change with the forecast horizon (figure 1*a*). Given the stochastic nature of population fluctuations, it is not possible to predict exactly how the population will change in the future.
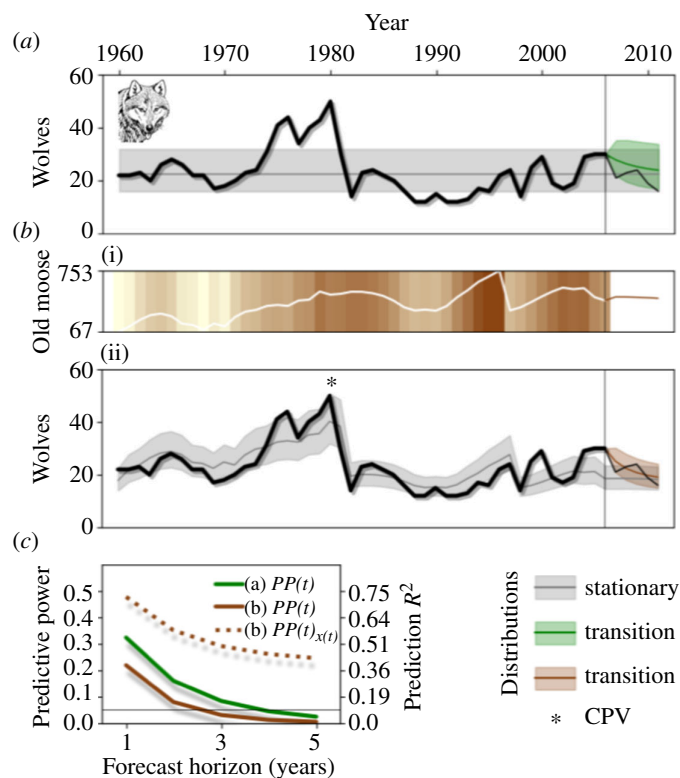
Figure 1. The main elements characterizing intrinsic predictability. (*a*) Panel depicting the abundance time series of the wolf population on Isle Royale (black line, 1959–2011) with the stationary and transition distribution. For illustrative purposes, we take the year 2006 as the 'current' year to make predictions. (*b*) Panel (ii) depicting the analogous situation as in (*a*), except that now two explanatory variables—moose population (old, i.e. senescent, moose (i)) and effects of canine parvovirus (CPV; asterisk in (ii))—are used. The stationary and transition distributions are therefore conditional on the covariates. (*c*) Panel showing intrinsic predictive power, $PP(t)$ (box 1), for the analyses (*a*,*b*) and forced predictive power, $PP_x(t)$ (box 2), for the analysis with explanatory variables (*b*). All distribution variances in (*a*,*b*) are visualized as 66% confidence intervals. Drawing: Pearson Scott Foresman, public domain.

Box 1. Intrinsic predictive power

Predictive power, $PP(t)$, can be easily formulated for Gaussian processes like widely used time-series models. For a univariate time series (electronic supplementary material, appendix 1.1, equation (S1)),

$$PP(t) = 1 - \left(\frac{v(t)}{v_\infty}\right)^{1/2}, \tag{2.1}$$

where $v(t)$ and v_∞ are the variances of the transition and stationary distributions and t is the forecast horizon. Calculation of $v(t)$ and v_∞ is outlined in electronic supplementary material, appendix 1.1. The formula can be extended to include estimation uncertainty in model parameters used to calculate $v(t)$ and v_∞ [30]. Generally, $PP(t)$ declines over time (i.e. forecast horizon), eventually approaching zero: in this limiting case, $v(t) = v_\infty$ and predictability is lost (figure 1*c*). For univariate processes, $PP(t)$ is related to the theoretical limit of forecast accuracy, $R_{pred}^2(t) = 1 - v(t)v_\infty^{-1}$ [37], as $R_{pred}^2(t) = 1 - (1 - PP(t))^2$. The link between $PP(t)$ and forecast accuracy as measured by $R_{pred}^2(t)$, and the decrease of predictability over time theoretically confirms previously proposed but unresolved hypotheses [35].

Because equation (2.1) is suitable for Gaussian processes, time-series models from the ARMA(p,q) family are apt candidates for implementing $PP(t)$. For the purpose of assessing predictability, it is convenient to state an ARMA(p,q) process as a dynamic regression model:

$$y(t) = \mu(t) + \varepsilon(t), \tag{2.2}$$

$$\varepsilon(t) = \sum_{i=1}^{p} b_i \varepsilon(t-i) + \sum_{j=0}^{q} a_j \vartheta(t-j). \tag{2.3}$$

Here, $\mu(t)$ is the potentially time-varying process governing the mean of $y(t)$ (box 2) and $\varepsilon(t)$ are temporally autocorrelated errors; without a dependence of the mean on time, $\mu(t)$ is simply a constant (e.g. 'carrying capacity'). For a univariate ARMA model, $PP(t)$ depends on the $p + q$ ARMA coefficients (equation (2.3)), whereas the residual variance of the process (σ_ϑ^2) cancels out (electronic supplementary material, appendix 1.1). From a simulation study presented in electronic supplementary material, appendix 1.2, we recommend setting $q = 0$ for unbiased estimates of predictive power.

Box 2. Forced predictive power

The definition of predictive power can be extended for processes with a mean that changes with external, explanatory variables. A possible explanatory variable is time, allowing the incorporation of time trends. The simple case of a single explanatory variable can be expressed as

$$\mu(t) = c(\bar{x}(t) + \alpha(t)), \tag{2.4}$$

where $x(t) = \bar{x}(t) + \alpha(t)$ is broken down into deterministic and stochastic components. The regression coefficient c for $y(t)$ on $x(t)$ can be estimated from time-series data or treated as a known value for projecting different forecasting scenarios. Writing the process mean $\mu(t)$ as a linear function of $x(t)$ causes little loss of generality because an explanatory variable can be transformed to generate a linear relationship with $y(t)$. To be consistent with the ARMA approach we have taken (box 1), we assume that $\alpha(t)$ has a Gaussian distribution with variance v_x. Multiple explanatory variables can be incorporated similarly.

Changes in the mean $\bar{x}(t)$ and variation $\alpha(t)$ in $x(t)$ have different consequences for predictability. $PP(t)$ addresses the rate at which the transition distribution approaches the stationary distribution, where both distributions correspond to the variation in $y(t)$ around $\mu(t)$ given by $\varepsilon(t)$. Therefore, $PP(t)$ does not include variation in $y(t)$ created by variation in $\mu(t)$. When predictions are made conditional on a specific future value of $x(t)$ and when a researcher wants to incorporate the information this provides into predictive power, then the appropriate reference stationary distribution becomes the distribution of $y(t)$ around $\bar{\mu}(t) = c\bar{x}(t)$ rather than $y(t)$ around $\mu(t)$. The stationary distribution of $y(t)$ around $\bar{\mu}(t)$ has variance $v_T = v_\infty + c^2 v_x$, which is always greater than v_∞ for $c \neq 0$. When there are changes in $\bar{x}(t)$, the 'forced predictability' is

$$M(t) = (\bar{\mu}(t) - \bar{\mu}(0))^2 (2v_T)^{-1}, \tag{2.5}$$

which is derived for Gaussian processes from the Kullback–Leibler divergence (or relative entropy) between the current distribution of $y(0)$ and the distribution of $y(t)$ [38,39].

Incorporating both the mean and variation in $x(t)$ gives a measure of predictive power for explanatory variables (see also [38]):

$$PP_x(t) = 1 - \exp(-M(t))\left(\frac{v(t)}{v_T}\right)^{1/2}. \tag{2.6}$$

If there is no variation in $x(t)$, then $v_T = v_\infty$ and equation (2.6) gives the effects of pure forcing of the process through changes in $\bar{\mu}(t)$. If there is no change in $\bar{\mu}(t)$, then $\exp(-M(t)) = 1$ and $PP_x(t)$ is similar to $PP(t)$, but with v_T replacing v_∞. Finally, if only the effect of forcing through changes in $\bar{\mu}(t)$ is of interest, then $v(t)$ can be set equal to v_T; this case we define as $PP_M(t)$.

Nonetheless, for a density-regulated population, it is possible to predict the overall tendency—the mean of the transition distribution approaches the stationary mean—and the uncertainty around this tendency, captured by the variance of the transition distribution around its mean. Thus, starting at the current abundance, the transition distribution will change through time and eventually converge to the stationary distribution. These two distributions—transition and stationary—are the main elements characterizing predictability: the less the transition distribution overlaps with the stationary one, the more predictive information is available for reliable forecasts based on the present state of the population, and predictability is high [31].

The predictability measure we use is the metric predictive power, $PP(t)$, rooted in information theory and developed in climatology to measure the uncertainty in predictions [30] (box 1). Previous work on predictability in ecology has used model-free methods based on information theory [29,32] or computational irreducibility [28], methods that typically cannot be integrated into further modelling and forecasting for biodiversity conservation. Predictive power, $0 < PP(t) < 1$, depends on the forecast horizon t—in this study, time in years—and $PP(t)$ will decrease to zero as t increases to infinity and the transition distribution converges to the stationary distribution (figure 1c). In practice, it makes sense to define a predictability barrier that gives a threshold below which the predictability of the system is negligible. To cast predictability in familiar statistical terms, $PP(t)$ can be shown to be related to the theoretically maximum possible prediction R^2 reflecting forecast accuracy (box 1). Using this link, to determine a predictability barrier, we will use $PP(t) = 0.05$ as a threshold, corresponding to a maximum possible prediction R^2 of approximately 10% for univariate time series (figure 1c). The selection of a threshold should change depending on a researcher's needs. Here, we have selected a low threshold because, even with this low threshold, many of the time series we analysed reach this threshold in only a few years; if we selected a higher threshold, the resolution would not be high enough to separate predictive power for many time series. Finally, where it is necessary to distinguish it from other predictability metrics, we will refer to $PP(t)$ as the *intrinsic* predictive power because it only depends on the variation of the observed data.

We implement $PP(t)$ using time-series models from the ARMA family [40] (box 1). ARMA models are familiar to many ecologists and evolutionary biologists (e.g. [41]) and are used extensively owing to their parsimonious and flexible nature. ARMA models make it possible to address many central topics in wildlife data, ranging from measurement error to population decline owing to human stressors. ARMA models are often accurate approximations to nonlinear systems [40], although for highly nonlinear processes like systems with multiple stable states (however elusive these are [42]), ARMA models will fail to capture patterns caused by the nonlinearities and therefore may underestimate the true predictability of the data. This might

argue for an approach that computes the information content of a dataset without the need to specify a model [29,32]. The cost of taking a model-free approach, however, is that there is no way to directly translate these information-based metrics into terms that assess model fit and predictive ability.

(a) Broad comparisons of predictability among species

To gain a bird's-eye view on the predictability of animal population sizes and phenotypes, we analysed 320 invertebrate and 963 vertebrate ecological time series from the following four taxonomic groups: insects, birds, mammals and fish. Invertebrate data were collected either at the species level or at the sample plot level (total abundance or biomass, but not species richness or similar), and data of the other three groups were all collected at the species level [43,44] (electronic supplementary material, figure S3, table S1, appendix 4). We also analysed 307 phenotypic time series of bird, fish, and mammal populations [45] (electronic supplementary material, figure S3, table S3 and appendix 4). For selecting datasets, we used the following criteria (electronic supplementary material, appendix 4): (i) only yearly data; (ii) no presence–absence data; (iii) a minimum length of 20 years for ecological data and 15 years for phenotypic data owing to the smaller amount of time series available; (iv) a maximum proportion of missing values of 25%; and (v) a maximum of five consecutive missing values. In electronic supplementary material, appendix 4, we address time-series length and predictability in more detail. As for potential time trends, we ran analyses using no, linear or quadratic time trends (electronic supplementary material, appendix 4). All analyses were performed using Python [46]. Although for this broad comparison we analysed population-level data without explicitly considering additional abiotic and biotic variables, for simplicity we will broadly refer to these population-level dynamics as ecological dynamics and phenotypic dynamics. Later on (§2d), we will additionally consider covariate data, where the term ecological dynamics more correctly applies (instead of population dynamics).

(b) Multivariate time series

Sometimes, multiple correlated time series are available, for example, for an ecological community or for different phenotypic measures from the same organism. Predictability as measured by $PP(t)$ is defined for the multivariate case and can be applied to multivariate ARMA(p,q) models (electronic supplementary material, appendix 1.1). The univariate formula (box 1) is just a special case [30].

When multiple time series are available, they could each be analysed separately, they could be analysed as a multivariate set or a dimensionality reduction method like principal components analysis (PCA) could be applied and a univariate analysis on a single dimension conducted. Which approach is best? There is no simple answer, and the best approach will depend on the time series and objectives. To illustrate the three approaches, we use a phenotypic dataset of beak morphology of three populations of Darwin's finch species on Daphne Major Island for the period 1973–2012 [47] (electronic supplementary material, figure S2 and appendix 4).

(c) Predictability of exploited populations

People worldwide rely on and benefit from the use of about 50 000 wild species for food, medicine and recreation [48]. Unfortunately, exploitation has become a main cause of elevated extinction risk, affecting species from many faunal and floral taxonomic groups [4,49,50]. Wildlife management has increasingly sought harvesting strategies to minimize overexploitation, and nowadays many approaches include forecasting population dynamics to abide by sustainable management [23,51,52].

We expect the predictability of exploited populations to reflect life history characteristics: because larger animals tend to be exploited relatively more often [53] and their life history characteristics correlate with a decreased degree of density dependence [54], this will lead to higher predictability (box 1). But different harvesting strategies can also affect predictability (box 3). To illustrate how management affects predictability, we analysed data from 13 Swiss cantonal populations of the northern (Alpine) chamois (*Rupicapra rupicapra*) for the years 1980–2020, for which hunting returns and abundance time series are available [55] (electronic supplementary material, appendix 5.2).

It is important to note that management strategies that lead to greater predictability are not necessarily indicators of good management. High predictability implies that more information about future abundances is available from information about the present state of the population, and if a good management strategy compensates rapidly when there is overexploitation, the desired rapid return of the population to its stationary distribution would associate low predictability with good management.

(d) Predictability of forced systems

So far, we have not considered the possibility of external or environmental variables that affect either the mean or variation of the variable of interest. If, for example, the mean abundance of a population depends on the mean annual temperature, then how would knowledge of this dependence affect our ability to predict the future mean population abundance under different scenarios of global warming? Similarly, if temperature affected the year-to-year variation in the abundance of a population, then how does knowledge of temperature in a given year help us predict the population abundance in that year? Here, we address predictability for forced systems—systems that depend on external variables—which have been largely ignored in the ecological predictability literature [29,35].

Box 3. Harvesting strategies and predictive power

A convenient way to categorize harvesting strategies is by expressing annual harvest, $H(t)$, as the product of the proportion of the population harvested, $p(t, N(t))$, and population size, $N(t)$: $H(t) = p(t, N(t))N(t)$, where $p(\cdot)$ is a function of $N(t)$. We consider the case in which $p(t, N(t))$ can be approximately expressed as a linear function of $y(t) = \ln(N(t))$, so that $H(t) = (h_0 + h_1 y(t) + \hbar(t))N(t)$ and $\hbar(t)$ are the residuals of the fitted proportion. If $h_1 = 0$, we recover the abundance-independent proportional strategy. For $h_1 > 0$, the proportion harvested increases with increasing $N(t)$, and the intercept h_0 influences the threshold below which no animal is harvested. Finally, $h_1 < 0$ gives a linear approximation to a constant yield strategy at equilibrium, $p(t, N(t)) = Q(t)N(t)^{-1}$, where $Q(t)$ is the constant yield. This model for a harvested population generates the autoregressive parameter b_1 that depends on the harvesting parameter h_1, $b_1 = (1 - h_1 e^{-\beta})(1 - \gamma)$, where β is the birth rate and $(1 - \gamma)$ is the autoregressive parameter of the unharvested population (electronic supplementary material, appendix 5.1). Because parameter b_1 directly affects predictability (box 1), harvesting strategies with $h_1 \neq 0$ will do the same. As detailed in electronic supplementary material, appendix 5.1, while this approach gives a linear approximation of widespread harvesting strategies, the results might not apply to highly nonlinear systems.

To avoid confusion about the meaning of 'prediction', we distinguish between explanatory and anticipatory predictions [56]. Explanatory predictions are tested with observed data, whereas anticipatory predictions forecast future states of the system; the concept of predictability involves anticipatory predictions. If knowledge can be obtained about external variables affecting observations (explanatory predictions), then these might be used for making anticipatory predictions. Therefore, we have incorporated external variables into a measure of forced predictive power, $PP_x(t)$ (box 2 and figure 1b).

If an external variable $x(t)$ explains in part patterns in the observations of a time series $y(t)$, to make multi-year forecasts of $y(t)$, the future values of the mean of $x(t)$ would ideally be known. While in many situations these values will be unknown, values of $x(t)$ might be assigned to make forecasts under different scenarios for the future, such as different projections of future global warming or different assumptions about habitat degradation. Furthermore, it might be possible to predict future values of $x(t)$ from the existing data (figure 1b). Finally, time can be treated as an external variable, making it possible to ask how predictability changes when there is a time trend in the population's mean. In all of these situations, the goal is to determine the maximum anticipatory predictability when the mean value of $x(t)$ changes.

Predictive power can be expanded to account for year-to-year variation in $x(t)$. The effects of this variation on $y(t)$ are often studied using observed data for explanatory prediction, although conceptual issues must be addressed to use the results in anticipatory prediction. Predictive power $PP(t)$ (box 1) addresses the information provided by the observed values of $y(t)$ on future values of $y(t)$ that depend on the variation in the future values around the mean of $y(t)$; in other words, $PP(t)$ concerns predictability given by the transition distribution of the residual variation in $y(t)$ that is not explained by $x(t)$. When variation in $x(t)$ drives variation in $y(t)$ and future values of $x(t)$ are unknown, then the explanatory predictability provided by $x(t)$ does not aid in anticipatory predictability, and therefore the explanatory predictability of $x(t)$ should be ignored. However, this seems to throw away information that $x(t)$ provides about $y(t)$. Our measure of forced predictive power, $PP_x(t)$ (box 2), addresses this by using observations to compute the conditional predictability of a future value of $y(t)$ given that $y(t)$ is predicted once the value of $x(t)$ for that year is known. This formulation of $PP_x(t)$ guarantees that as $x(t)$ provides greater explanatory predictability of the observed data, $PP_x(t)$ increases.

To illustrate $PP_x(t)$, we performed univariate analyses of the three beak measures of the medium ground finch (*Geospiza fortis*) we described in §2b. Moreover, for a broader view, we analysed the ecological and phenotypic datasets time series with statistically detectable time trends. We selected these 948 time series from the 1590 time series described in §2a.

3. Results

(a) Broad comparisons of predictability among species

For the 1283 ecological and 307 phenotypic analysed time series, we found that 50% of all time series are predictable at most 1 year ahead, with interquartile ranges of 0–3 years and 0–2 years, respectively (electronic supplementary material, figure S4). Because values of the predictability barrier and 1-year-ahead predictive power, $PP(1)$, are strongly associated (Spearman's ϱ = 0.95, $p < 0.0001$), in figure 2 we present $PP(1)$ values separated by taxonomic groups and for ecological time series also by illustrative subgroups/families. The results indicate that mammal populations have the highest predictability, followed by fishes, birds and insects (ecological data only). All results combined (grey lines in figure 2), 50% of ecological and phenotypic time series have a $PP(1)$ value of at most 0.13 and 0.06, respectively: $PP(1) = 0.1$ translates to a maximum possible 1-year-ahead prediction R^2 of ~20% (box 1), for the modest endeavour of predicting next year's ecological or phenotypic population value.

For ecological time series, the dependence of $PP(1)$ on ecological characteristics (figure 3) gives some interesting lessons for conservation. Time series from protected areas had on average the same predictive power as those outside protected areas (figure 3b), and primary threats (human stressors) and the total number of threats [4] (electronic supplementary material, table
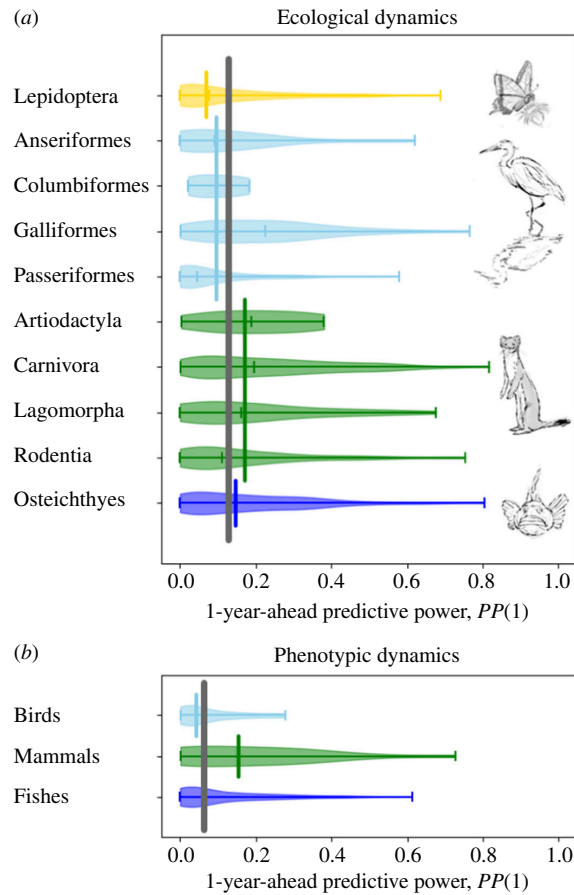
Figure 2. Predictability across animal populations. The distributions of 1-year-ahead predictive power values, $PP(1)$, are shown for (*a*) ecological and (*b*) phenotypic population time series, sorted into the taxonomic groups insects (only *a*), birds, mammals and fish, and in (*a*) additionally sorted into 10 illustrative taxonomic subgroups. For each taxonomic group, a vertical line gives the median value over all respective populations; smaller vertical lines give the median and minimum/maximum values. In (*a,b*), the overall median value is marked with a vertical grey line. Drawings: Andrea Klaiber, © Wildlife Analysis GmbH, Switzerland.

S2) were not associated with predictive power (electronic supplementary material, figure S5). Therefore, as a group, species of conservation concern are neither more nor less inherently predictable than other species, leading to two corollaries. First, making predictions for species of concern presents no special challenges, at least from the perspective of population dynamics. Second, the threats themselves do not seem to create unpredictability in population dynamics. Comparing across habitat realms, the freshwater time series of all taxonomic groups have the lowest predictive power (figure 3*a*), implying that these species are more susceptible to annual environmental fluctuations. This is noteworthy because freshwater populations have been suffering the most pronounced human-driven declines [17]. An additional useful result in practice relates to data aggregation (figure 3*c*): for insects, the degree of data aggregation (single species versus sample plot abundance or biomass) seems not to influence predictive power. This result contrasts with previous studies arguing that aggregated data may be expected to be more predictable ([35] and references therein). Finally, across the globe (figure 3*d*), populations along the Pacific coast in the northern hemisphere show relatively low predictive power, a pattern driven mainly by fish populations (electronic supplementary material, figure S6). To better understand this pattern, in electronic supplementary material, appendix 4, we present preliminary statistical evidence showing that predictability may in part be driven by a population's food web embedding, supporting a previously published hypothesis ([35] and references therein).

(b) Multivariate time series

Analyses of three beak measures of the medium ground finch (*G. fortis*) and small cactus finch (*Geospiza scandens*) gave similar results for all three approaches employed to investigate the potential advantage of a multivariate analysis (figure 4): analysing traits separately, first performing a PCA and using the first component, and analysing all three traits together. For the large ground finch (*Geospiza magnirostris*), however, the multivariate assessment leads to greater predictive power; this implies that there is information in the co-variances between the traits that are not incorporated into univariate analyses.

This example illustrates that, while there is no guarantee that a multivariate approach provides higher predictive power, it would be prudent to try a multivariate analysis. A multivariate approach will be especially worth trying within conservation projects involving management areas, as opposed to projects focusing on single species. If a project's success in a management area depends on its ability to protect multiple species—or aggregate measures of ecosystem health such as carbon sequestration and nutrient run-off prevention—then multivariate predictive power gives an assessment of how well the outcome of management goals can be predicted. In sum, multivariate predictive power provides a potential holistic assessment of the ability to make predictions.
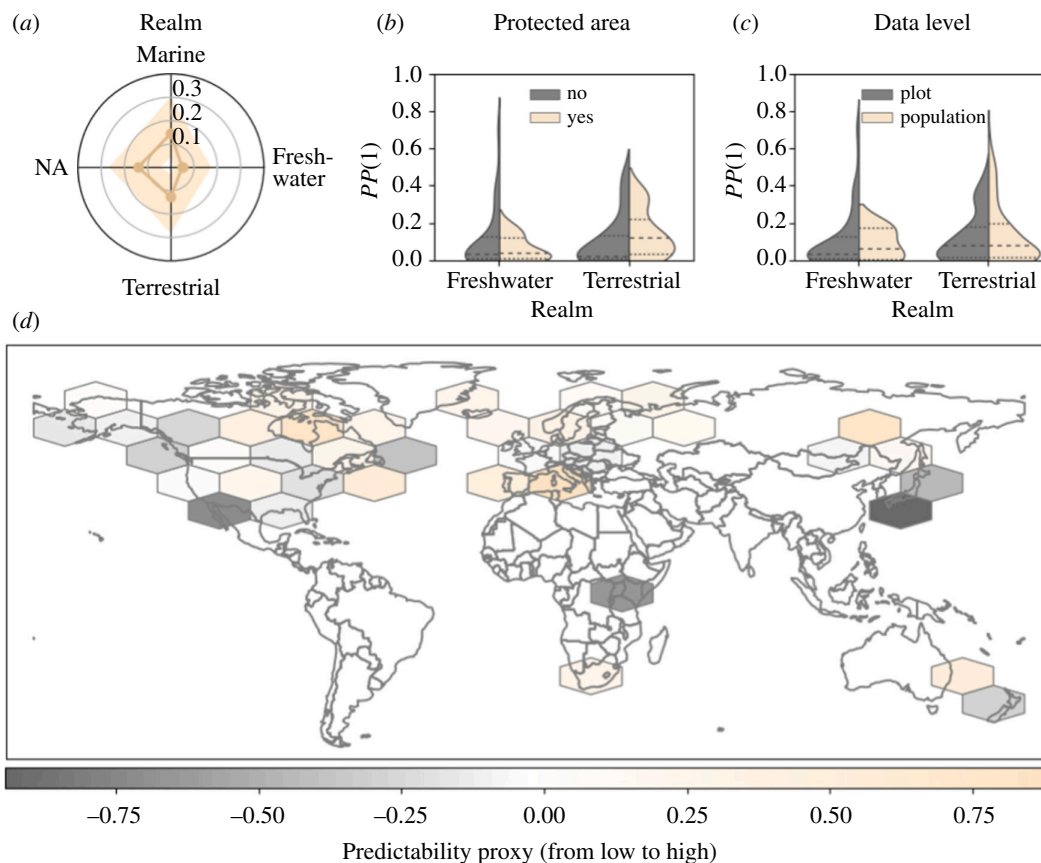
Figure 3. Global predictive power of ecological dynamics. (*a*) Panel summarizing the 1-year-ahead predictive power values, $PP(1)$, sorted by realm (median and interquartile range). (*b*,*c*) Panels depicting the distribution of $PP(1)$ values of insects, sorted by protection status and data level (species or plot time series), respectively (median and interquartile range), in both cases further classified by realm. (*d*) Panel depicting, as a hexagonal grid, a summary of geographically sorted $PP(1)$ values (see colour bar).
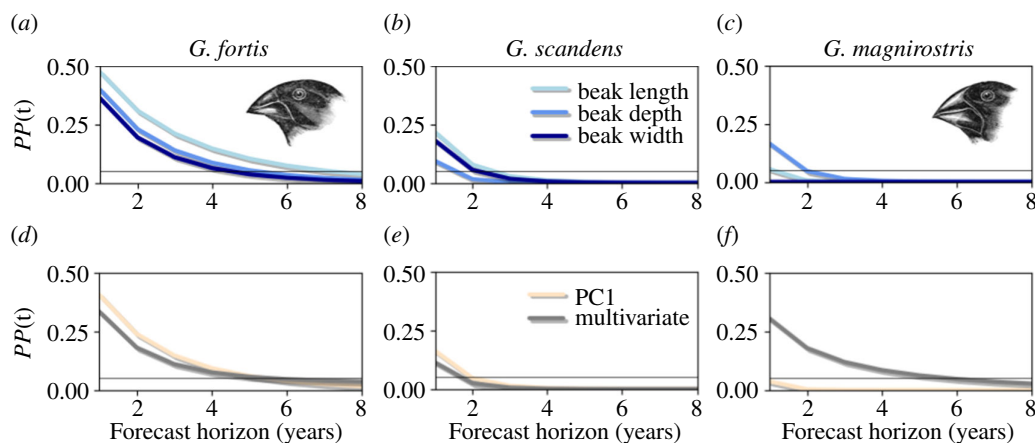
Figure 4. Predictability of univariate versus multivariate time series. (*a*–*c*) Predictability results for each finch species (column title) with all three measures analysed separately. (*d*–*f*) Analogous results based on the first component of a PCA (PC1) and the multivariate assessment. Drawings: John Gould, public domain.

(c) Predictability of exploited populations

The distribution of 1-year-ahead predictive power values, $PP(1)$, of 13 Swiss chamois populations reveals no intuitive geographic pattern (figure 5*a*). The harvesting strategy captured by the harvesting parameter h_1 (box 3), however, shows a clear effect on predictive power (figure 5*b*). For populations subject to a harvesting strategy in which the proportion harvested is adaptively adjusted according to the current abundance ($h_1 > 0$), predictive power is lower, while populations subject to constant yield-like harvesting ($h_1 < 0$) have higher predictive power. This result occurs because the state-dependent management approach tracks the yearly population dynamics to decrease the variation in population fluctuations, which thus decreases predictability (box 1). In contrast, a constant yield-like harvesting strategy does not dampen population fluctuations but instead increases them relative to the mean population by depressing the population, thereby increasing predictability. Other species and management strategies might give different patterns. We cannot claim generality from this single example. Nonetheless, the example shows that predictive power is not an immutable property of a population or phenotypic trait but instead depends on the forces that affect populations, including management strategies.

For conservation, the chamois example shows that low predictability is associated with better management. High predictive power implies that there is a lot of information in the residual, unexplained variation in a population. Thus, the residual information revealed by high predictive power is information that has not been used in the management strategy. A state-dependent harvesting strategy is more likely to lead to sustainability and reduced extinction risk [51], and the lower predictive power caused by such a strategy is an indication that management is effective.

(d) Predictability of forced systems

For the time series of the three beak measures of the medium ground finch, beak depth and width decreased over time, while beak length showed no time trend (electronic supplementary material, figure S2). Therefore, we compared the intrinsic and forced predictive power for these time series (figure 6). For both beak depth and width, the intrinsic predictive power $PP(t)$ remains above the threshold 0.05 (§2) for 4 years. As $PP(t)$ decreases, the forced predictive power caused by the time trend, $PP_M(t)$ (box 2), increases, crossing the threshold at 2 and 4 years for beak depth and length, respectively. The increase in $PP_M(t)$ occurs because, as the predicted means of beak depth and length increase above the observed values, the predicted means provide more information. The differing patterns of $PP(t)$ and $PP_M(t)$ show a switch in information useful for making predictions. For the first 4 years, $PP(t) > PP_M(t)$, implying that information about the last observations provides better predictions, while afterwards, $PP(t) < PP_M(t)$, implying that using information about the time trends will provide better predictions.

For all ecological and phenotypic time series with time trends, we computed the number of years before $PP_M(t) > 0.05$, the time at which information about the time trend provides substantial predictive power. For approximately half of the time series, the time trend remains unpredictable for at least 1 year and potentially many more years (figure 6c,d and electronic supplementary material, figure S8).

4. Discussion

For any biodiversity change assessment, the first step should be to evaluate predictability. Predictive power, $PP(t)$, gives an objective summary of the information content in the data and a first cut at more detailed modelling to make predictions. $PP(t)$ focuses on the 'unexplained' variation in a time series that is not associated with any explanatory variable, asking whether this variation can be used for predictions (box 1). We also present $PP_x(t)$ that incorporates explanatory variables $x(t)$ (box 2). If $x(t)$ accounts for some of the observed variation in a time series, then $PP_x(t)$ will be greater than $PP(t)$. $PP_x(t)$ can also be used to assess predictions made from time trends in data. Thus, $PP(t)$ and $PP_x(t)$ parse out where informative patterns exist in time-series data, directing attention to how reliable and credible predictions can best be made.

The predictability measure $PP(t)$ is generic, in the sense that it can be applied to any time series or simultaneously to multiple time series. Our finding that the predictability of the ecological and phenotypic data collections was similar in magnitude surprised us (figure 2), because we expected population-level phenotypic changes to be too slow to be detectable in most time-series datasets. However, if the fitness consequences of traits are large, then traits should change on similar time scales to population abundances [26]. Less surprising were the generally low $PP(t)$ values (figure 2), confirming previous findings in ecology [28]: in ecological systems, low predictability is assumed to be pervasive owing to the complexity of ecological systems involving many species with different behaviours, physiologies, etc. Differences in $PP(t)$ among time series may also reflect heterogeneity in quality among time series and their short lengths. This underscores the need to compute $PP(t)$ in biodiversity conservation where time series of interest are often short and of suboptimal quality [15]. Low $PP(t)$ values also caution against further statistical analyses and argue for future concerted efforts to obtain information to increase predictive power; a 'better model' will be of little help for data that are inherently unpredictable.

Is high predictive power 'good' for conservation management? High $PP(t)$ values imply that a mathematical/statistical model can be used to predict future values because information about the present state of the system is 'remembered' in the future. While the ability to make good predictions is valuable, the same memory will make a system slow to respond to conservation management strategies. Thus, high predictability measured by $PP(t)$ might make it difficult to detect responses of populations to conservation actions, hindering adaptive management. To obtain a more complete and broadly applicable assessment of predictability, we defined $PP_x(t)$ that explicitly incorporates explanatory variables (figure 1b) and time trends (figure 6).

Biotic data for explanatory variables might not be widespread in conservation studies except for well-studied and monitored systems (e.g. [36,47]). Abiotic data for explanatory variables, however, may be readily available or even be routinely collected (e.g. data on temperature and precipitation trends or land-use change [44]). Furthermore, time trends can and should be investigated for a predictability assessment, as illustrated by our detection of time trends in 948 of 1590 ecological and phenotypic time series. We cannot give general recommendations for how much effort should be devoted in a study towards obtaining information about explanatory variables $x(t)$ versus obtaining better time-series data on the focal variable $y(t)$. This will depend on the costs and benefits for a given study. Nonetheless, $PP(t)$ and $PP_x(t)$ give the tools to assess the possible benefits of obtaining explanatory variables. Both $PP(t)$ and $PP_x(t)$ can be calculated with available data, and values of $PP_x(t)$ substantially greater than $PP(t)$ would argue for devoting more effort to obtaining information about $x(t)$.

For conservation management, our analyses of the 1590 ecological and phenotypic time series give a striking contrast between intrinsic predictive power, $PP(t)$, and predictive power generated by a time trend, $PP_M(t)$. The intrinsic predictability barrier was greater than 1 year for only 50% of the time series, implying that current observations provide information for at most short-term predictions. However, for 50% of the 948 time series with time trends, $PP_M(t)$ exceeded the same threshold in
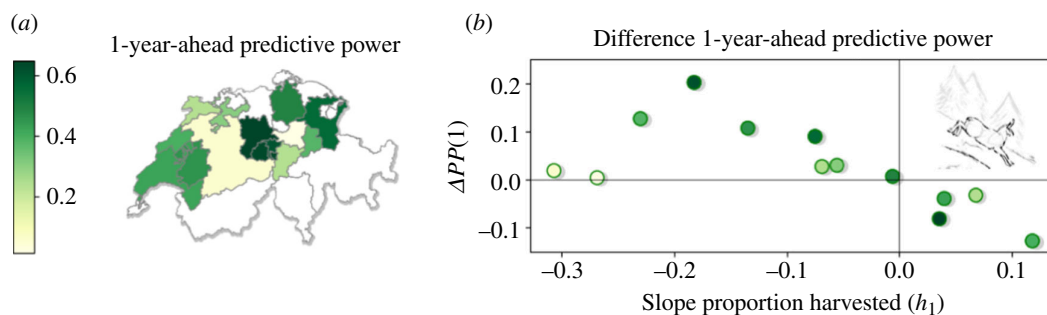
Figure 5. Effect of harvesting strategy on predictability. (*a*) Panel geographically presenting estimated 1-year-ahead predictive power values, *PP*(1), of 13 Swiss cantonal chamois populations. (*b*) Panel illustrating the change in the 1-year-ahead predictive power, Δ*PP*(1) (harvested minus non-harvested), as a function of the harvesting strategy characterized by the slope value (h_1) on the *x*-axis (i.e. how the proportion harvested depends on abundance; box 3). The dot colours are the same as in (*a*). Drawing: Andrea Klaiber, © Wildlife Analysis GmbH, Switzerland.
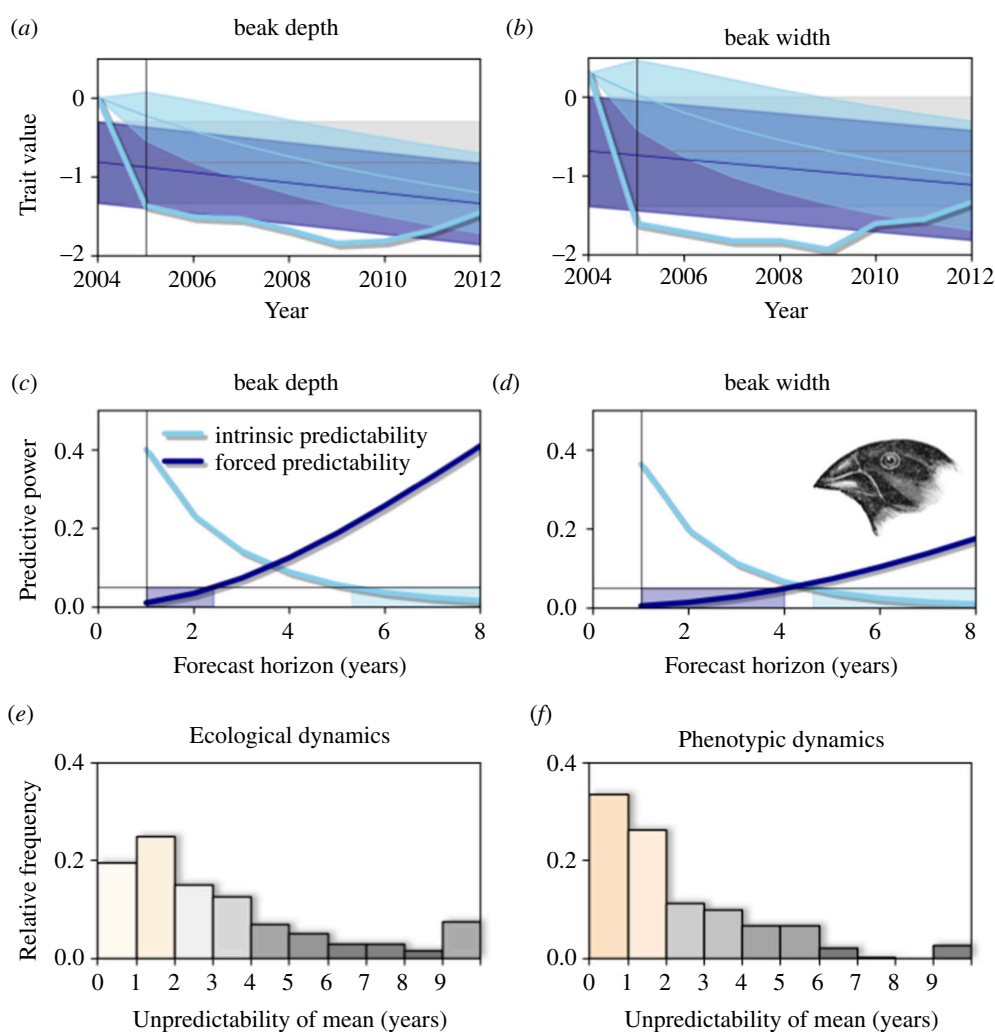
Figure 6. Predictability of forced systems. For beak depth and width of the medium ground finch (*G. fortis*), panels (*a*,*b*) depict the *z*-transformed data (2004–2012; electronic supplementary material, figure S2), the current stationary distribution (in grey), the forced stationary distribution (dark blue) and the transition distribution (light blue). All distribution variances are visualized as 66% confidence interval. (*c*,*d*) Panels showing the predictive power, *PP*(*t*), and explanatory predictive power, $PP_M(t)$ (box 2), with the coloured areas corresponding to the unpredictable period of the forced (dark blue) and intrinsic (light blue) predictive power, respectively. In (*a*–*d*), the current year is assumed 2004, from which forecasts would be made. (*e*,*f*) Panels showing the duration of the initial unpredictable period of the forced predictability (see the dark blue areas in *c*,*d*) for all (*e*) ecological and (*f*) phenotypic time series with a time trend. Drawing: John Gould, public domain.

2 or fewer years. In other words, for many time series, the information provided by an estimate of the time trend exceeded that provided by the last observations after only a few years. Of course, the predictive power of recent observations versus time trends will depend on the time series under study, and time trends may be transitory and changeable. Nonetheless, our results argue that, if there is a time trend, it may provide more information for making even short-term forecasts than current observations.

Many authors have encouraged conservation scientists and practitioners to incorporate predictions into the management cycle (e.g. [19,56] and references therein). A predictability assessment should help to interpret these predictions in a realistic and

useful way for decision-making. For example, conservation prioritizations should include forecasting to identify populations of greatest need of interventions. Predictive power can help to assess which population-level predictions are more 'trustworthy' (i.e. have high predictive power). The distribution of $PP(t)$ values among taxonomic groups (figure 2) suggests that it is possible to adopt group-specific predictive approaches. For example, many insect populations show low intrinsic predictive power (figure 2), making forecasts for insect populations more challenging: in these cases, directing the focus to forced predictability may be sensible.

Predictions can also benefit the selection and implementation of conservation actions [19]. For example, the expected effect of suitable conservation actions on future population dynamics could be compared, and the resulting ranking could be further weighted by the respective resources needed. The assessment of predictability at the implementation stage will be especially valuable when thinking about monitoring the expected action-specific outcomes. A declining population represents a forced system (box 2), and many conservation actions aim at halting or reversing declines. Forced predictive power, $PP_x(t)$, gives a metric to ask how quickly changes in a forced stationary distribution—forced by conservation actions—will be predictable. In many of the analysed time series with a time trend (figure 6), a changing mean can be detected in only a few years. Such an analysis for a specific conservation programme will give a time frame for when a conservation action might be deemed a success or failure or help ranking different conservation actions. This approach differs conceptually from an impact assessment based on a counterfactual analysis, increasingly employed in a conservation context ([19] and references therein). To compute forced predictability (box 2), the current (observed) stationary distribution is compared with the time-varying (predicted) forced stationary distribution, the latter being forced by conservation actions. For an impact assessment, in contrast, the forced stationary mean is compared to a counterfactual population trajectory, i.e. the time-varying predicted dynamics if no actions were implemented. We feel that comparing one forced (action-driven) trajectory to the current (observed) population state is more prudent than comparing it to a second, non-measurable counterfactual trajectory.

As scientists worried about biodiversity loss, we often call for more and higher-quality data; what we really want are data that contain more predictive information. Given the urgency for action dictated by a rapidly changing world, we need to use the hard-won data we already have and explore ways of extracting predictive information from these data: we cannot afford to wait for 'better' data to become available while human-caused stressors are downgrading wildlife populations and habitats. We believe that embracing the concept of predictability will benefit the urgent and global endeavour of protecting life on Earth.

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