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From here and now to there and then: Practical recommendations for extrapolating cetacean density surface models to novel conditions

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LIVING MARINE RESOURCES PROJECT 31
DenMod: Working Group for the Advancement of Marine Species Density Surface Modeling

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[1] http://navysustainability.dodlive.mil/files/2018/01/LMRFactSheet_Project31.pdf

[2] http://navysustainability.dodlive.mil/environment/lmr/

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Acronyms

AFTT	Atlantic Fleet Training and Testing (area)
CBD	Convention on Biological Diversity
DSM	Density Surface Model
EBV	Essential Biodiversity Variable
EEZ	Exclusive Economic Zone
ESA	Endangered Species Act
GAM	Generalised Additive Model
GEO BON	Group on Earth Observations Biodiversity Observation Network
IUCN	International Union for the Conservation of Nature
LMR	Living Marine Resources
MMPA	Marine Mammal Protection Act
NAEMO	Navy Acoustic Effects Model
ONR	Office of Naval Research

Executive summary

Density surface models (DSMs) are clearly established as a method of choice for the analysis of cetacean line transect survey data, and are increasingly used to inform risk assessments in remote marine areas subject to rising anthropogenic impacts (e.g. the high seas). However, despite persistent skepticism about the validity of extrapolated models, more and more DSMs are being applied well beyond the boundaries of the study regions where field sampling originally took place. This leads to potentially uncertain and error-prone model predictions that may mislead on-the-ground management interventions and undermine conservation decision-making. In addition, no consensus currently exists on the best way to define and measure extrapolation when it occurs, leaving users without the tools they require to audit models projected into novel conditions. Consequently, a transparent and consistent protocol for identifying scenarios under which extrapolation may be appropriate (or conversely, ill-advised) is urgently needed to better gauge how models behave outside the boundaries of sample data and to know how much faith can be placed in their outputs.

This report aims to address this gap by synthesising recent advances in extrapolation detection, and presenting recommendations for a minimum standard for measuring extrapolation in novel environmental space. Such guidelines are essential to promoting transparency, replicability, and quality control, and will help marine scientists, managers and policy agencies to (i) better interpret density surfaces and their associated uncertainty; (ii) refine model development and selection approaches; and (iii) optimise the allocation of future survey effort by identifying priority knowledge gaps, e.g. by delineating areas where model predictions are the least supported by data. Our review is accompanied by supplementary R code offering a user-friendly framework for quantifying, summarising and visualising various forms of extrapolation in multivariate environmental space *a priori* (ahead of model fitting). We illustrate its application with case studies designed to revisit previously published predictions of sperm whale (*Physeter macrocephalus*) and beaked whale (*Ziphiidae spp.*) densities in the Northwest Atlantic, and evaluate them in light of several extrapolation metrics.

Very early in their training, ecologists are given strong warnings against extrapolating, as model predictions made in data-deficient contexts rely heavily on assumptions that may not hold outside the range of sampled conditions. Navigating the ‘uncharted waters’ of extrapolation, however, is critical to scientific progress, and will be best achieved with a clear understanding of the mechanics, benefits, and limitations of extrapolated models.

1. Introduction

The expanding footprint of human activities across the world's oceans is rapidly creating novel challenges for the conservation of marine vertebrate populations globally (Lewison et al. 2014; Halpern et al. 2015). With more than a quarter of all extant cetacean species (i.e. whales and dolphins) currently believed to face extinction (Davidson et al. 2012), geographically-explicit risk assessments are urgently required to mitigate the cumulative impacts of anthropogenic threats such as fisheries bycatch, noise pollution, and climate change, amongst numerous others (Avila et al. 2018). Reliable estimates of cetacean abundance or density patterns in both space and time are fundamental to addressing this need, but remain difficult to obtain in many marine areas subject to limited sampling effort (e.g. the high seas; Kaschner et al. 2012).

In this context, the development of predictive statistical models that can estimate cetacean abundance as a function of spatially- and temporally-referenced environmental covariates – both static (e.g. seabed depth and slope) and dynamic (e.g. sea surface temperature, primary productivity) – has greatly accelerated over the last decade (Guisan & Zimmermann 2000; Guisan & Thuiller 2005; Redfern et al. 2006; Ready et al. 2010; Dambach & Rödder 2011; Robinson et al. 2011, 2017; Marshall et al. 2014). In particular, GAM[3]-based density surface models[4] (Hedley & Buckland 2004; hereafter DSMs; Miller et al. 2013) are now clearly established as a method of choice for the analysis of cetacean line transect surveys in the presence of imperfect detectability, and provide useful tools for generating policy-relevant knowledge in support of applied management against a backdrop of data deficiency (Becker et al. 2012; Hammond et al. 2013; Redfern et al. 2017; Derville et al. 2018). For instance, DSM outputs have recently been used to guide the designation of marine protected areas (e.g. Cañadas & Vázquez 2014), inform the rerouting of major shipping lanes (e.g. Redfern et al. 2013), assist the planning of military exercises (e.g. Mannocci et al. 2017b), or forecast cetacean population dynamics in the face of extreme weather events (Becker et al. 2018).

Immediate and pressing demands for solutions to large-scale management problems are increasingly encouraging the application of ecological models well beyond the boundaries of the study regions where sampling originally took place (Miller et al. 2004; Sequeira et al. 2018a), such that many cetacean DSMs involve some degree of extrapolation (e.g. Mannocci et al. 2015; Virgili et al. 2018; García-Barón et al. 2019). Very early in their training, scientists are warned against extrapolating (Conn et al. 2015a), as inference outside the range of the sample relies on fundamental assumptions that lack direct empirical support from the available data (Elith & Leathwick 2009; Escobar et al. 2018; Qiao et al. 2019) and may lead to extreme predictions with only limited biological realism (Owens et al. 2013). Accordingly, most models

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[3] GAM: Generalised additive models (see Wood 2017 for technical details).

[4] Two or more stage modelling framework combining a spatial model of abundance with a detection function model of sighting distances to correct for uncertain detection.

transferred into novel temporal and/or spatial domains are expected to be fraught with both statistical and ecological errors (Clark et al. 2001; Peters & Herrick 2004), the magnitude of which can vary substantially across taxonomic groups, habitats, and/or modelling algorithms (e.g. Fielding & Haworth 1995; Shabani et al. 2016; Redfern et al. 2017). It is unsurprising, therefore, that appropriate evaluations of model prediction uncertainty and extrapolative capacity under previously un-encountered environmental scenarios are rapidly emerging as an active and important area of research in applied ecology and conservation (Steen et al. 2017; Yates et al. 2018).

1.1 Scope

As acoustically-specialised animals, cetaceans are sensitive to the negative effects of chronic and acute exposure to man-made underwater noise (Williams et al. 2015). For instance, the noise generated as a by-product of commercial maritime traffic or seismic exploration can mask species' acoustic communication signals, disrupt diving behaviour, elicit physiological stress, and/or cause displacements from favoured habitats, ultimately interfering with key life functions such as foraging, mating, nursing, and/or resting (Tyack 2008; Erbe et al. 2018; Gordon 2018; Wensveen et al. 2019). Intense impulsive sounds from high-power mid-frequency naval sonar have also been linked with atypical mass stranding events in several species (Jepson et al. 2003; D'Amico et al. 2009; Filadelfo et al. 2009) and are thus of serious concern, although available evidence from controlled exposure experiments suggests that measurable behavioural responses may vary between and within individuals and populations (e.g. DeRuiter et al. 2013; Goldbogen et al. 2013; Southall et al. 2016; Harris et al. 2018). In recognition of anthropogenic underwater noise as a world-wide problem, a rising number of calls are being made to strengthen management and mitigation frameworks for sound-producing activities (Dolman & Jasny 2015).

In the United States, the Marine Mammal Protection Act of 1972 (MMPA, 16 U.S.C. 1361 et seq.) regulates the 'take' (i.e. the harassment, hunting, capture, or killing) of marine mammals by U.S.-based organisations anywhere around the globe, including areas beyond national jurisdiction (i.e. on the high seas; Mannocci et al. 2017b). The U.S. Navy is legally bound to comply with the MMPA and other U.S. Federal laws (e.g. the Endangered Species Act ESA 16 U.S.C.1531 et seq.) pertaining to protected marine species, and thus required to determine the effects of Systems Command military readiness training exercises on whales and dolphins, particularly where those involve the use of active sonar and the deployment of explosives and munitions. To this end, the U.S. Navy designed a simulation tool, the Navy Acoustic Effects Model (NAEMO), which quantifies the likely number of impacted individuals based on sound propagation models and predicted density maps for all species known to occur within affected areas (Ciminello et al. 2013). Reliable estimates of cetacean density (and how these fluctuate spatio-temporally) are thus needed in locations where Navy training and testing occurs. When these locations have not been surveyed for marine mammals, then density estimates are usually obtained from DSMs extrapolated from adjacent sampled areas.

1.2 Objectives

A transparent and uniform approach to quantifying extrapolation is a critical prerequisite to furthering our understanding of how models may behave outside the bounds of the data from which they are built (Escobar et al. 2018), and therefore to knowing how much credence or skepticism their outputs should be given. Although several extrapolation metrics have already been proposed in the peer-reviewed literature (e.g. Elith et al. 2010; Rödder & Engler 2012; Zurell et al. 2012; Mesgaran et al. 2014; Conn et al. 2015a), little consensus exists on which proves most appropriate for a given dataset, with limited clarity on how extrapolation affects predictions generated by models developed from different types of data (e.g. abundance vs. presence-only data). In particular, general rules for supporting consistent assessments of extrapolation remain lacking in cetacean studies, prompting an urgent need to standardise best practice in model evaluation (Sequeira et al. 2018a).

The purpose of this report is to propose a series of practical guidelines for diagnosing, measuring, and visualising extrapolation in novel multivariate environmental space. While our primary focus is on density surface models of cetacean populations, the general concepts and software tools presented herein are equally relevant to other types of models, and applicable to other taxa or other forms of biological data. Note that we concentrate on extrapolation as defined by Strong & Elliott (2017), i.e. the estimation of a response function (empirical or mechanistic), that allows predictions of an ecological variable to be obtained based on a set of observations and a number of predictor (explanatory) covariates. Other approaches to ecological scaling do exist (e.g. lumping) but are not dealt with here (see Strong & Elliott 2017 for details). Furthermore, given inherent variability in the predictive performance of different model algorithms (Meynard & Quinn 2007; Rapacciuolo et al. 2012; Beaumont et al. 2016; Yates et al. 2018), we only consider extrapolation assessments performed *a priori*, i.e. before model fitting. As such, the extrapolation detection approaches described below can only be used to identify *potential* areas where model predictions may be prone to errors. The magnitude of these errors, or their associated uncertainty, is however likely to differ between model types and parameterisations. Notwithstanding, we expect that standard guidelines for quantifying extrapolation will assist marine scientists, managers and policy agencies in:

- Better interpreting model predictions (e.g. density surfaces) and their associated uncertainty;
- Refining model development and selection protocols accordingly;
- Targeting future survey effort by identifying priority information gaps and delineating areas where model predictions are least supported by data.

The report is structured as follows:

- The next section contains an overview of extrapolation in novel environmental space. In it, we define and illustrate various extrapolation scenarios, explain why extrapolating is critical (and inevitable) in many cetacean studies, and succinctly review the range of extrapolation diagnostics currently available, highlighting two that are of particular value for use with DSMs. In addition, we list the key assumptions made when projecting models into novel conditions to improve awareness of the potential pitfalls associated with extrapolation.
- Following from this, we briefly describe a set of custom functions developed in the programming language R (https://cran.r-project.org/) to assist extrapolation assessments in DSMs and other predictive models. We provide links to the code, which draws upon real-world abundance data from line transect surveys of cetaceans undertaken aboard shipboard and airborne sampling platforms across portions of the U.S. and Canada's Exclusive Economic Zones (EEZ) (equivalent to ca. 1.1 million linear km of total effort; **Fig. 1**). Survey details and data sources are fully described in Roberts et al. (2016) and Mannocci et al. (2017b).
- We conclude the report by offering general guidelines on how to approach extrapolation detection in DSMs and outlining priority areas for future research.

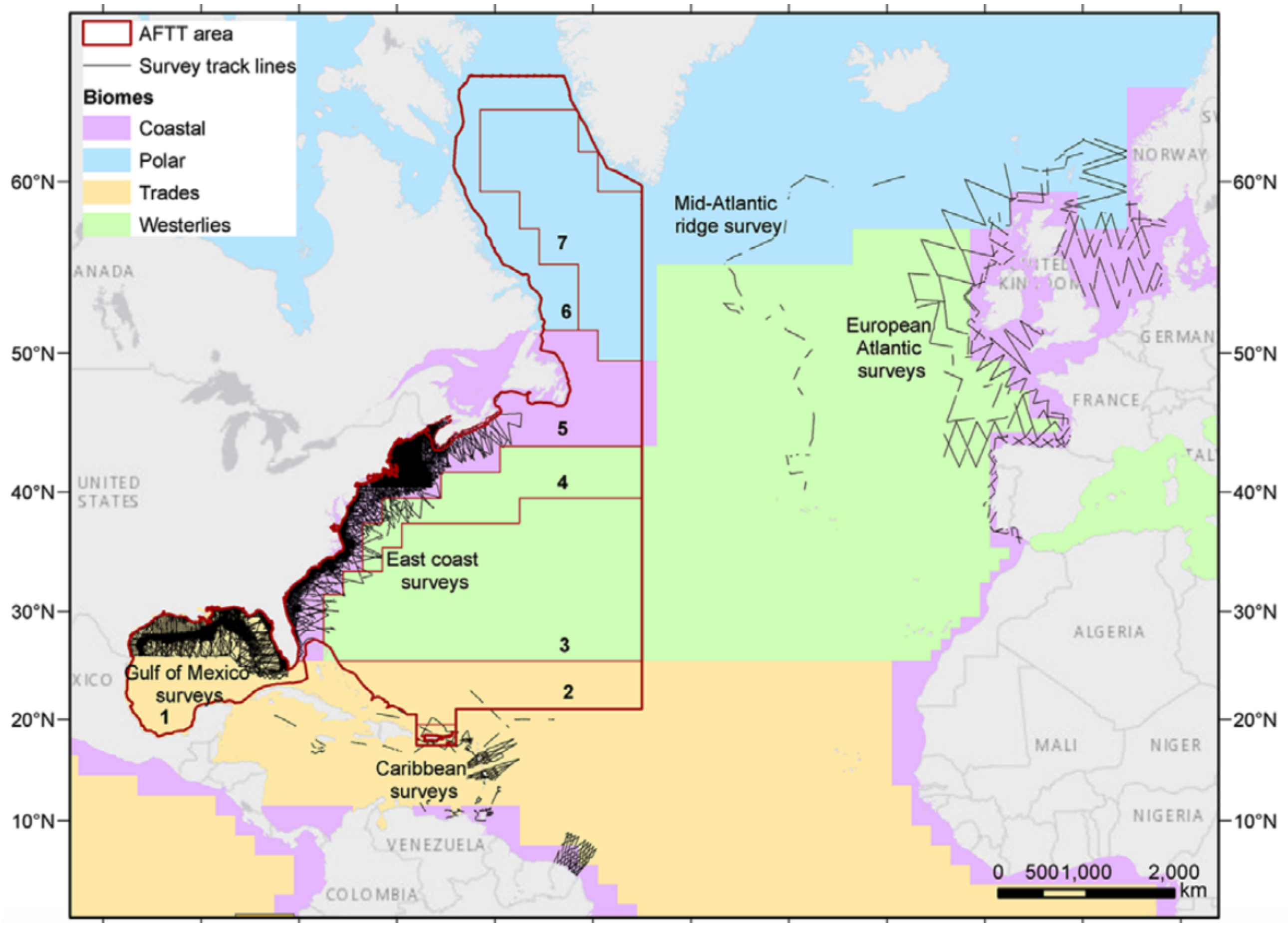

Figure 1: Map of cetacean line transect surveys conducted in the North Atlantic basin (including the U.S. EEZ and Gulf of Mexico). The U.S. Navy Atlantic Fleet Training and Testing (AFTT) area (which excludes territorial waters <12 nautical miles of the shore) is shown as a red outline (11 x 10^6 km^2). Line transect surveys for cetaceans appear in black. Colours and numbers represent distinct biomes and biogeographical provinces, respectively. Data sources are detailed Mannocci et al. (2017b) and Roberts et al. (2016). Figure reproduced from Mannocci et al. (2017b) under a Creative Commons Attribution 4.0 International License CC BY 4.0.

2. A short review of extrapolation in environmental space

2.1 Definition

To extrapolate means:

'*To project or expand existing knowledge in order to generate insights about an unknown system, based on an assumed continuity, correspondence, or other parallelism between it and the observed data.*' (Miller et al. 2004).

Put simply, extrapolating is the act of using a point/region of reference[5], where baseline information exists, to estimate the value(s) of a variable at another target[6] point/region, which has not been sampled and for which predictions are sought (Munns 2002).

In ecology, extrapolation is typically performed over space (e.g. between regions differing in latitude and longitude), and/or over time (e.g. into the future or the past), although alternative forms of extrapolation are also commonplace in related disciplines (**Fig. 2**) (e.g. across taxonomic levels or ontogenetic stages in experimental biology and laboratory studies; amongst doses and exposure regimes in ecotoxicology) (Solomon et al. 2008). The magnitude (extent) of extrapolation can be conceptualised as a dissimilarity index (or distance) between target and reference systems (**Fig. 3**) in the multivariate space defined by their respective environmental conditions (Radeloff et al. 2015; Sequeira et al. 2018a). The greater this distance, the stronger the extrapolation. Note that, in this case, extrapolation is measured along the chosen environmental dimensions of interest, rather than in geographic (e.g. in km, using Cartesian coordinates) or temporal (e.g. hours, days, weeks) space (Booker & Whitehead 2018). This means that some extrapolations may fail immediately after the reference domain is abandoned (eg. in adjacent areas; Osborne & Foody 2007), or conversely, that others made across continents/ocean basins or through centuries are theoretically permissible so long as reference and target conditions are sufficiently similar (Yates et al. 2018).

Extrapolation is problematic for a multitude of reasons (see section **2.3**), and a growing body of literature now documents how ecological inference becomes perilous outside the scope of the data used for model training (Graf et al. 2006; Dormann 2007; Fisher & Naidoo 2011; Torres et al. 2015; Bell & Schlaepfer 2016; Péron et al. 2018). Part of the danger stems from the fact that even models that adhere closely to sample observations can yield misleading outputs if they fail to capture the underlying process that generated the data in the first place (Heikkinen et al. 2012). This is perhaps best understood in the context of a simple univariate regression analysis.

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[5] Also referred to as 'source', 'training', 'internal' or 'calibration' system/domain.

[6] Also referred to as 'test', 'external', 'evaluation', 'candidate' or 'projection' system/domain.

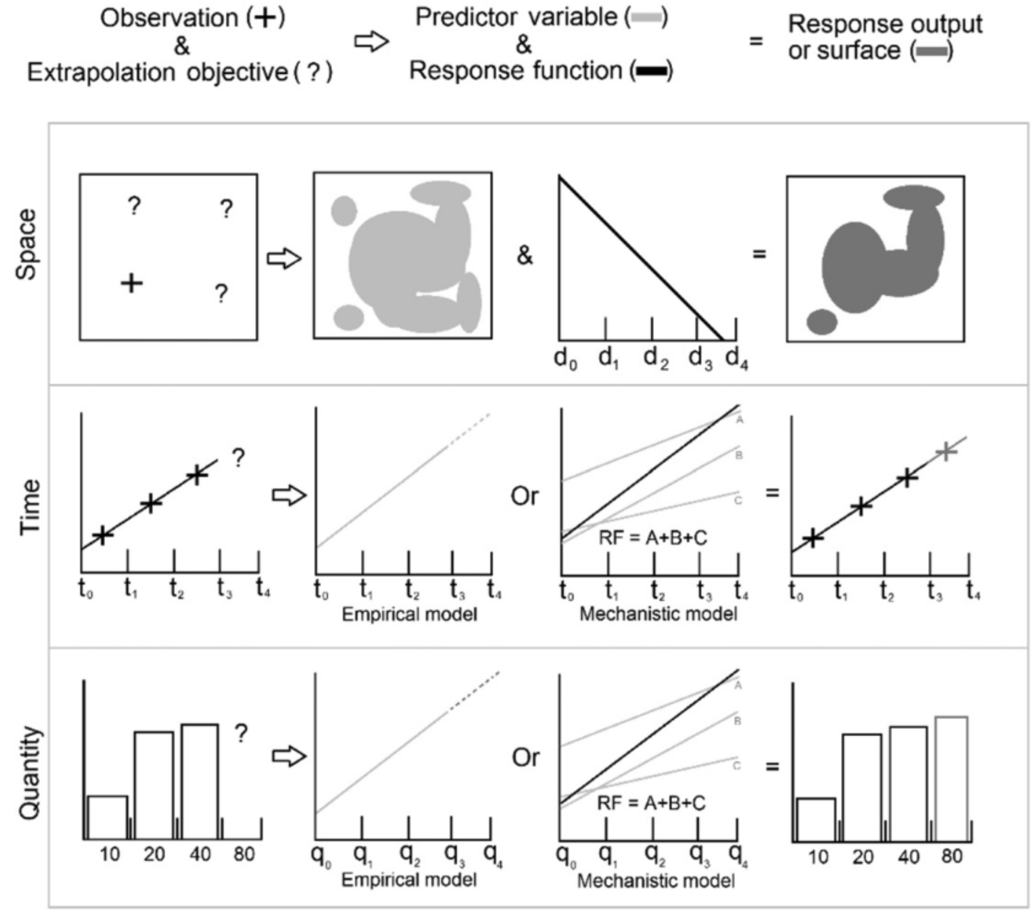

Figure 2: Basic types of extrapolation. Spatial and temporal extrapolations (top and middle) are common in ecology, and are the focus of the present report. Figure reproduced from Strong & Elliott (2017) with permission from Elsevier.

Fig. 4 shows a linear model of the body growth of North Atlantic right whales (*Eubalaena glacialis*) based on length-at-age data obtained from both live and necropsied individuals (Fortune et al. 2012). Here, estimates of juvenile and adult (Phase II) body sizes from calf growth rates (Phase I) are positively biased, leading to over-predictions for animals older than ca. one year of age. The potential for extrapolated models to yield biologically implausible results (Owens et al. 2013) calls for vigilance when inferring the value of a dependent variable Y_i beyond the range of independent variables, i.e. when $X_i < \min(X)$ or $X_i > \max(X)$ (Conn et al. 2015a). Importantly, the above example demonstrates how good model fit (e.g. here, $R^2 > 0.85$) is not synonymous with, nor sufficient to guarantee, satisfactory predictive performance (Araújo et al. 2005; Guisan et al. 2017; Petitpierre et al. 2017; Sequeira et al. 2018a).

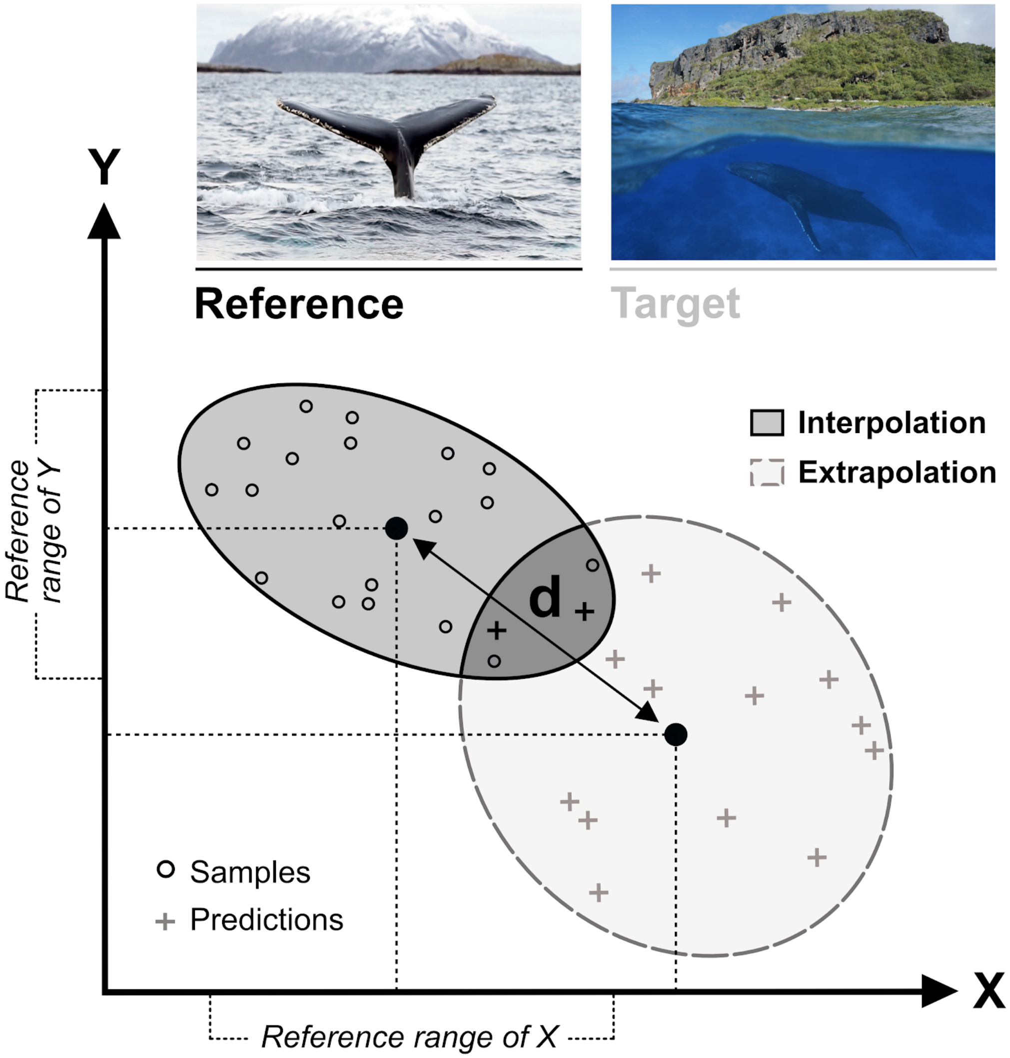

Figure 3: Schematic representation of extrapolation in the environmental space defined by two hypothetical biotic/abiotic covariates relevant to humpback whales (*Megaptera novaeangliae*), as an illustrative example. Here, X and Y may correspond to known ecological drivers of whale density such as water temperature and krill abundance, and exhibit different ranges of values in the animals' high-latitude polar feeding grounds (reference system) vs. their low-latitude, warm-temperate breeding grounds (target system). The shaded areas denote the envelopes (or hypervolumes) of the reference (calibration) and target (prediction) data along the dimensions of X and Y. Prediction points that overlap or fall outside the dark grey ellipsoid are classed as 'interpolations' and 'extrapolations', respectively. The magnitude of extrapolation can be intuitively viewed as the multivariate distance or dissimilarity, *d*, between reference and target systems. Figure inspired by Sequeira et al. (2018a). Photo credits: Buendia Photography (left), Wild Earth Expeditions (right).

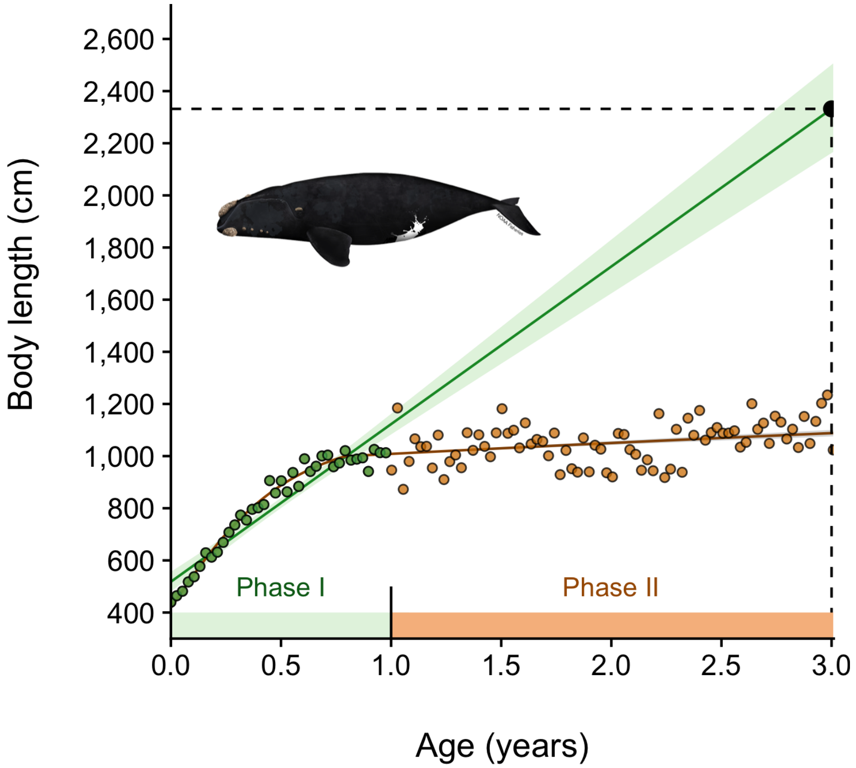

Figure 4: Example of errant extrapolation in the estimation of North Atlantic right whale (*Eubalaena glacialis*) size as a function of age. The species exhibits differential growth rates at various stages of maturity, with calves gaining considerable mass while nursing (a daily average of ~1.7 cm and ~34 kg during the first twelve months of life; Phase I), and growing much more slowly thereafter (Phase II). Despite an excellent fit (adjusted $R^2 = 0.89$), a simple linear model fitted to Phase I data only ignores the asymptotic nature of growth and substantially overpredicts the body length of mature individuals (e.g. 23.3 m at 3 years of age, 95% CI 21.6 - 25 m, i.e. larger than some subspecies of blue whales). Data from Fortune et al. (2012). Right whale silhouette credits: NOAA Fisheries (https://www.fisheries.noaa.gov/).

2.2 Why extrapolate?

Extrapolation has two primary motivations in ecological research.

Firstly, the conservation challenges burgeoning in the Anthropocene have forced ecologists to contend with issues that manifest at increasingly large scales spanning thousands of kilometres and unfolding over decades to centuries (Scholes 2017). However, logistical constraints and modest budgets tend to limit field sampling to relatively small areas and short time horizons, creating a mismatch between available capacities, and current needs, for data collection. To this day, much of the biosphere thus remains under-explored and inadequately known (Whittaker et al. 2005; Brito 2010; Bland et al. 2017), even where high-quality research infrastructure is readily available (Butler et al. 2010), with one in six species (of 13,465) on the International Union for Conservation of Nature (IUCN) Red List still classed as Data-Deficient (Bland et al.

2017). Knowledge gaps are most prevalent in marine systems, especially in the deep pelagic ocean (Webb et al. 2010; Kaschner et al. 2012; Bouchet 2015), which is remote and inaccessible, and across the EEZs of many developing countries (Jarić et al. 2014), where financial resources are insufficient for even basic information on species occurrence to be gathered (Braulik et al. 2018). Such levels of data deficiency pose a serious roadblock to furthering progress towards meeting the Convention on Biological Diversity's (CBD) Aichi Targets, as they compromise estimates of extinction risk and lead to many little known organisms being overlooked in conservation planning (Bland et al. 2015; Walls & Dulvy 2019). In many situations where data simply do not exist, extrapolation therefore represents a practical inevitability, and an essential component of criteria setting in ecological risk assessments. Unsurprisingly, the use of extrapolative models has experienced explosive growth in recent decades, particularly by governmental and non-governmental organisations charged with natural resource and endangered species management at large spatial scales (Franklin 2010a).

Secondly, the latter half of the 20th century saw a paradigm shift in the philosophy of science from *explanatory* to *anticipatory* predictions (sensu Mouquet et al. 2015). This shift largely reflected the collective realisation that global change is fuelling increasing levels of novelty in ecosystems everywhere (Radeloff et al. 2015), giving rise to both abiotic and biotic conditions that are outside the range of historical baselines and may be without any analogues on the planet today (Williams & Jackson 2007; Fitzpatrick & Hargrove 2009). A pervasive issue for modern ecologists therefore lies in forecasting the future trajectories of ecosystems under human-mediated disturbance, but based on contemporary observations that can only offer an incomplete picture of how organisms may respond to conditions that do not presently exist (Fitzpatrick et al. 2018). For instance, with rising trends in the incidence of biological invasions worldwide, there is now renewed focus on preventative/mitigation measures aimed at detecting potential sites suitable for nonindigenous species establishment and spread (e.g. the Antarctic; Duffy et al. 2017). This implies a strong reliance on the extrapolation of parameter values beyond those available for model development and calibration within native habitats (Williams & Jackson 2007; Elith et al. 2010). Similarly, anthropogenic warming has already resulted in dramatic shifts in the range margins of numerous marine taxa (Perry et al. 2005; Laidre et al. 2008; Poloczanska et al. 2016), a trend likely to keep accelerating as temperature anomalies and extreme weather events become more frequent and longer-lasting (MacLeod 2009; Lambert et al. 2014; Cheung et al. 2015; Becker et al. 2018; Frölicher et al. 2018; Oliver et al. 2018). Understanding the extent to which species distributions may be affected by temperature fluctuations over the course of this century and beyond is thus pivotal to developing optimal management plans for the most vulnerable organisms (Beaumont et al. 2016). This is far from trivial, not least because climate velocity (i.e. the rate and direction of climate shifts) has been shown to vary substantially (Pinsky et al. 2013), and even species capable of rapid evolutionary adaptation may not track those changes appropriately (Bradshaw & Holzapfel 2006; Robinson et al. 2009). In the global ocean, an inherently dynamic environment subject to planet-level changes, forecasting without extrapolation may therefore be altogether unfeasible (Berteaux et al. 2006).

In the face of unabated marine and terrestrial defaunation crises (Dirzo et al. 2014; McCauley et al. 2015), enormous challenges remain for even simply assessing progress towards meeting the CBD's Aichi Targets, particularly on a global scale (Kissling et al. 2018). As a result, the concept of essential biodiversity variables (EBVs) was proposed by the Group on Earth Observations Biodiversity Observation Network (GEO BON) in 2013 as a harmonised system for delivering aggregated data on major dimensions of biodiversity loss and change (Pereira et al. 2013; Schmeller et al. 2017). Population abundance is one of 22 such EBVs (Kissling et al. 2018) and is a useful metric that can underpin assessments of extinction risk for threat categorization (Butchart et al. 2010), and serve as an early signal of the relative severity of expected impacts to ecosystems (Kulhanek et al. 2011). However, despite its obvious value to policy and decision-making (e.g. Acevedo et al. 2014), knowledge of population abundance remains scant for the majority of species (Bowler et al. 2019). This is in great part due to the difficulties of making accurate counts of organisms in the field, compared to simply recording their presence. As a consequence, abundance models usually entail a significant amount of spatial and temporal extrapolation, and remain more challenging to fit for many (marine) taxa (Sequeira et al. 2018b). That said, the superior information content associated with abundance data is expected to enhance transferability, so that extrapolated models of abundance, when available, might be better projected into non-analogue conditions than say, presence-absence models (Howard et al. 2014).

Many marine mammals, including cetaceans, are wide-ranging, highly mobile, cryptic, rare, and thus hard to survey, such that ca. 40% of extant species are currently inadequately known (Schipper et al. 2008). More than a third (36%) are also long-distance migrants with specialised diets that undertake ocean basin-scale movements to exploit seasonally available habitats and resources in multiple locations (Robinson et al. 2009). Ecological risk assessments for such data-poor 'moving targets' can seldom proceed without applying previously established ecological relationships to new areas, scales, and/or time periods (Clark et al. 2001), and extrapolation has therefore become commonplace in cetacean studies (Mannocci et al. 2015, 2017b; Roberts et al. 2016; Redfern et al. 2017), particularly where inference about broad-scale species distribution and abundance patterns is required to support on-the-ground management (Strong & Elliott 2017).

2.3 Error sources and assumptions

The pitfalls associated with extrapolating have been acknowledged in numerous disciplines (e.g. medicine, socio-economics, mathematics, engineering, biology) for over a century (Perrin 1904;

Thomas 1975; Riegelman 1979; Xiao & Yung 2015), and are covered in nearly every introductory statistics textbook (Zar 1999; Gillman 2009; Guisan et al. 2017). A telltale example of nonsensical extrapolation was provided in the early 1870s by Mark Twain:

"*In the space of one hundred and seventy-six years, the Lower Mississippi has shortened itself two hundred and forty-two miles. That is an average of a trifle over one mile and a third per year. Therefore, any person* [...] *can see that* [...] *a million years ago, the Lower Mississippi River was upward of one million three hundred thousand miles long, and stuck out over the Gulf of Mexico like a fishing rod. By the same token, any person can see that seven hundred and forty-two years from now, the lower Mississippi will be only a mile and three-quarters long, and Cairo and New Orleans will have joined their streets together, plodding comfortably along under a single mayor with a mutual board of aldermen.*"

Likewise, Von Foerster et al. (1960)'s tongue-in-cheek prediction that the world's human population would reach infinite size on November 13, 2026 - i.e. 'Doomsday' - was based on an extrapolation of growth models fitted to historical data. Clearly, extrapolations are sensitive and prone to a number of errors that may bias model outputs, impair prediction accuracy, and inflate uncertainty (Dormann 2007; Oliver & Roy 2015; Qiao et al. 2019) (**Table 1**).

Table 1: Common sources of errors encountered in ecological extrapolation.
Modified from Peters and Herrick (2004).

Error	Source
Measurement	Imperfect or imprecise sampling at discrete points in space or time.
Model	Wrong choice of particular model forms (equations) or components (variables, covariates).
Estimation	Statistical uncertainty in the estimation of model coefficients and parameters.
Process	Variability inherent to the system, especially expressed as 'natural' variation in variables or parameters of an implemented model.

Although the magnitude of errors is likely to vary amongst taxa, ecosystems, and/or modelling scenarios, most errors largely stem from violations of a number of key underlying assumptions (Richmond et al. 2010; Jarnevich et al. 2015; Guisan et al. 2017), including:

- **Equilibrium:** Species are often taken to be at equilibrium (or quasi-equilibrium) with their environment, meaning that they have colonised all suitable portions of their range and that occupancy or abundance data provide a direct representation of the species' fundamental niche (Araújo & Pearson 2005; Guisan & Thuiller 2005). However, suitable habitats may remain vacant if disturbance has eradicated populations from an area, if a species is expanding into habitats that have only recently become available, or if the regional population is insufficient to support colonisation (Wiens et al. 2009). Other factors such as group living and sociality, learning and memory processes, age or reproductive status-mediated habitat selection, migratory movements, dispersal lags or barriers, and biotic interactions (e.g. competition, predator avoidance, or pathogens) may also prevent individuals from accessing, or persisting in, suitable sites (Channell & Lomolino 2000; Svenning & Skov 2004; Václavík & Meentemeyer 2012). For instance, West Australian bottlenose dolphins (*Tursiops aduncus*) have been shown to remain in less prey-rich, but safer, shallow habitats during periods of high shark abundance (Heithaus & Dill 2006). Conversely, breeding-area philopatry and overcrowding in high-density populations may restrict some individuals to suboptimal conditions. Models developed in non-equilibrium settings (e.g. invasions, climate change) may thus involve biased records that are unrepresentative of species' habitat requirements and may lead to unreliable predictions (Elith & Leathwick 2009; Jachowski et al. 2016). Although this is an important assumption for transferring models in space or time, there have been surprisingly few critical appraisals of how close a given modelled system really is to equilibrium, or how long it would take to reach a new state of equilibrium, e.g. after environmental change (Guisan et al. 2017).

- **Adequate sampling:** Extrapolations are more likely to be spurious if samples themselves fail to encompass the full range of relevant environmental gradients present in the reference and target systems (Braunisch & Suchant 2010) (**Fig. 5**). Sampling effort varies across the globe, with much higher survey intensity in the vicinity of populated areas and in temperate regions (Anderson 2012). It is also common for ecologists to delineate their study areas arbitrarily according to geopolitical borders or other practical boundaries (El-Gabbas & Dormann 2018). Consequently, many biological datasets prove incomplete or exhibit spatial bias (e.g. Corkeron et al. 2011), resulting in models with truncated response curves that may under-represent areas of suitable habitats and suffer from limited predictive power (Vaughan & Ormerod 2003; Thuiller et al. 2004; Powers et al. 2011; Sánchez-Fernández et al. 2011).

- **Niche invariance:** Extrapolated forecasts rely on the principle of niche 'conservatism', i.e. the notion that ecological niches are a fixed and immutable characteristic of a species that remains stable over time and space, such that the factors that limit species' occurrence here today will be equally limiting elsewhere in the future (Martinez-Meyer et al. 2004). Recent reports of rapid niche shifts (Broennimann et al. 2007; Early & Sax 2014; Guisan et al. 2014) cast doubt on the validity of this assumption. In practice, model extrapolations are projections of the measured *realised* niche and may fail if these suitable habitats are not equally accessible across areas or time periods (e.g. due to different species assemblages and biotic interactions, or different geographic barriers to dispersal) (Guisan et al. 2017). Tests of niche equivalency (i.e. niches are strictly equivalent) and niche similarity (i.e.

niches are more similar to one another than to any random niche fitted in the same realised environment) can signal potential issues, but the former is usually so strict that it rejects niche overlap for most species, and the latter too liberal, such that even minute amounts of niche overlap will suffice for reference and target systems to be declared comparable (Guisan et al. 2017). A pragmatic yet data-intensive solution is to quantify the relationship between model extrapolation success and niche overlap. Where data availability allows such assessments, it is possible to use simple estimates of niche overlap as indicators of whether a model is likely to project well to a different area or time period (Guisan et al. 2017).

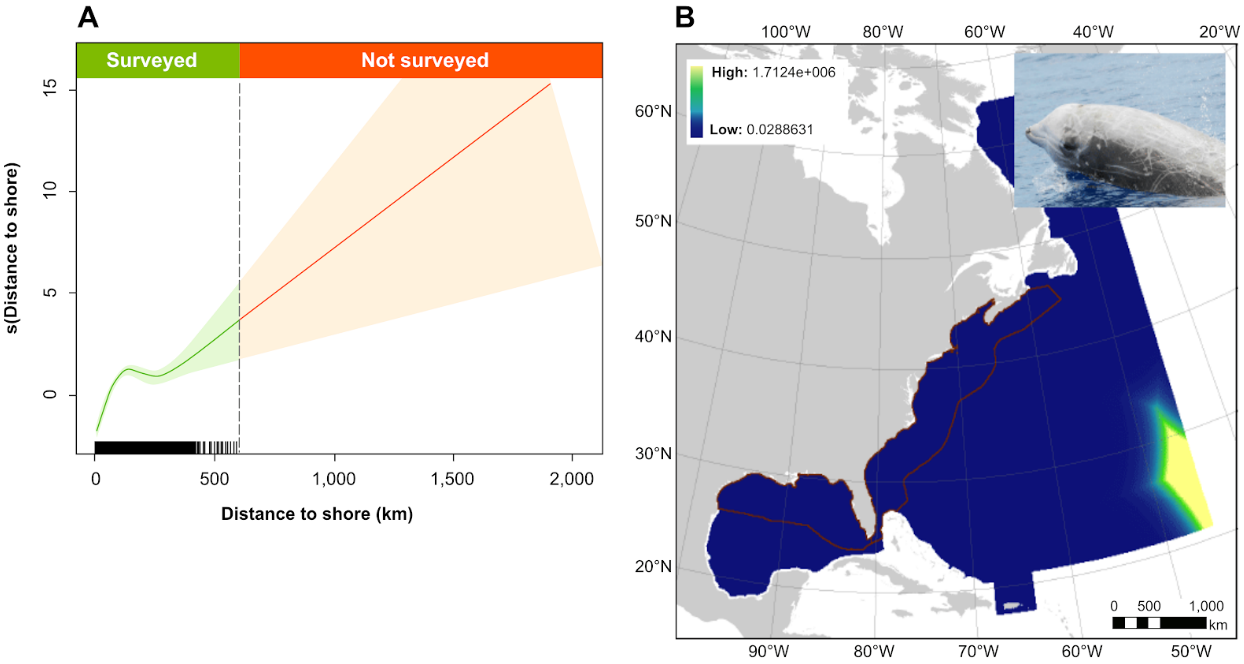

Figure 5: Real-world example of errant extrapolation in a density surface model of beaked whales (*Ziphiidae spp*) in the Northwest Atlantic Ocean. The model was developed from visual line transect survey data collected mostly within the United States and southern Canadian EEZs (red outline) and used to predict whale density across the larger Atlantic Fleet Training and Testing (AFFT) area. **(A)** Partial plot of the smooth term for distance to shore (solid line), with associated confidence intervals (shaded areas). Whale sightings largely occurred within ca. 500 km of the coast, but the model was projected into unsampled areas four times as distant. A linear extrapolation on the scale of the linear predictor led to an exponential increase in predicted whale density. **(B)** Resulting predictions are strongly biased towards the southeast corner of the study region, and exceed expected density values by several orders of magnitude, indicating serious extrapolation errors. Data courtesy of L. Mannocci and J. Roberts, Duke University.

- **Appropriate covariate choice:** The selection of adequate explanatory covariates is a prominent issue in predictive modelling (Wiens et al. 2009), which hinges not only on data availability but also on an understanding of the underlying mechanisms responsible for observed species' distribution and abundance patterns (Petitpierre et al. 2017; Fourcade et al. 2018). For instance, a frequent misconception is that species are exclusively affected by physical habitat features, when in fact their current distributions may also reflect historical human disturbance and landscape use (Fois et al. 2018). Extrapolations are likely to be particularly error-prone if distal (i.e. indirect) covariates are used, as correlations between these and true proximal drivers may fluctuate both spatially and temporally (Austin 2002; Yates et al. 2018). This may be exacerbated by measurement errors in covariate layers, an issue that has received limited attention in the predictive modelling literature (Guisan et al. 2017). Overall, important covariates that are unavailable should be identified *a priori*, and implications for model predictions anticipated (and discussed) to avoid drawing spurious conclusions (Guisan et al. 2017).

- **Stationarity:** For extrapolation to work, species-habitat relationships must be consistent and comparable in shape, direction, and amplitude within both the reference and target systems (the concept of "transportability"; Vaughan & Ormerod 2005). This implies that heterogeneity in both habitat availability and habitat selection between individual animals is deemed negligible (Osborne & Suárez-Seoane 2002), which is seldom reasonable. The assumption of stationarity also rarely holds for processes operating over large geographic areas or at fine resolutions (Unwin & Unwin 1998). With growing appetite for extrapolating models on global scales, there is a risk of including areas where animals respond to habitats in different ways (e.g. due to social status) (Osborne & Suárez-Seoane 2002).

- **Species isolation:** Biotic interactions (e.g. competition, predation, parasitism) have been shown to support key ecological and evolutionary processes and to play an essential role in structuring wildlife communities (e.g. Bateman et al. 2012; Morelli & Tryjanowski 2015; Atauchi et al. 2018; Palacio & Girini 2018), yet the majority of predictive models still largely ignore their effects, instead making the simplifying assumption that individual species exist in isolation and respond to their environment independently of each other (Wiens et al. 2009; Mpakairi et al. 2017). Increasing evidence of the potential for climate change to modify trophic relationships, trigger localised extinctions, or alter patterns of species dominance suggests that documenting and quantifying biotic interactions - although often an overwhelming task, even for a small number of species - may be necessary to support more robust extrapolation into novel contexts (e.g. Urban et al. 2012; Blois et al. 2013b; Alexander et al. 2015).

- **Adaptability:** Extrapolation assumes immediate adaptations to novel conditions, and while rapid evolutionary change is possible (Thompson 1998; Franks et al. 2007; Koch et al. 2014), it has only been empirically demonstrated in a few short-generation species. If species display high genetic, behavioural or phenotypic plasticity, extrapolation outputs may well be more variable (e.g. large predicted range) than under the assumption of genetic and phenotypic constancy (Rehfeldt et al. 2001).

- **Space-for-time substitutability:** Because long-term ecological time-series are generally rare, a common approach to performing temporal extrapolations is to develop models across multiple contemporary sites whose current conditions mimic the range of those known to have occurred in the past, or anticipated to arise in the future (Lester et al. 2014). The relationships identified across these spatial gradients are then used as surrogates for predicting temporal processes. Although successful in a number of cases (Banet & Trexler 2013; Blois et al. 2013a; Rolo et al. 2016), this approach could pose problems in non-stationary environments where the drivers of spatial and temporal turnover differ and where some of the key factors controlling population dynamics may remain unobserved but vary spatially (Damgaard 2019).

It is essential to understand the above assumptions, as failing to meet them can lead to both errors of omission (false negatives) and errors of commission (false positives) (Richmond et al. 2010; Sohn et al. 2013) that will undermine model interpretation. As an example, commission errors will lead to overestimations of species' range expansions in climate change studies, whereas omission errors will make range contractions appear more severe than they actually are (Rangel & Loyola 2012). Extrapolated models are particularly susceptible to the former, because the data used for model parameterisation seldom encompass the entire range of conditions present in the target region (Carneiro et al. 2016). Furthermore, extrapolation is risky in situations where response curves are high or increasing at the edges of the calibration domain (**Fig. 5**) (Peterson et al. 2011), and including descriptive spatial structures (e.g. via conditionally autoregressive models) can lead to misleading predictions of abundance around the edges of study areas (i.e. edge effects) or where there are large gaps in survey coverage (Ver Hoef & Jansen 2007; Conn et al. 2014, 2015b).

As ecological patterns, ecosystem dynamics, and species distributions and behaviours are governed by processes operating at multiple scales (e.g. Pirotta et al. 2014), careful attention should also be paid to the resolution (grain size) and the extent of both the response variable and predictive covariates in the reference and target systems (Kunin 1998; Miller et al. 2004). Some DSMs are projected onto rasters with an identical spatial resolution as that of the ones in which they were built (e.g. Mannocci et al. 2015). In other cases, however, extrapolations require traversing between different domains of scale, which brings the added complexity of having to account for localised sources of heterogeneity in each domain (Strong & Elliott 2017).

At coarser grains, the span of explanatory covariates decreases dramatically, such that two maps produced at different resolutions also exhibit different geographic extents and value ranges (Guisan et al. 2017) (**Fig. 6**). As a result, extrapolation errors are likely to arise when projecting a model fitted at a coarse grain to a finer grain (Randin et al. 2009). Hierarchical Bayesian frameworks offer one way of alleviating extrapolation issues associated with changes in grain size, e.g. by considering abundance at fine resolution as a latent variable that can be modelled as a function of fine-scale environmental covariates and constrained by observed abundances at coarser scales (see Keil et al. 2013 for an example).

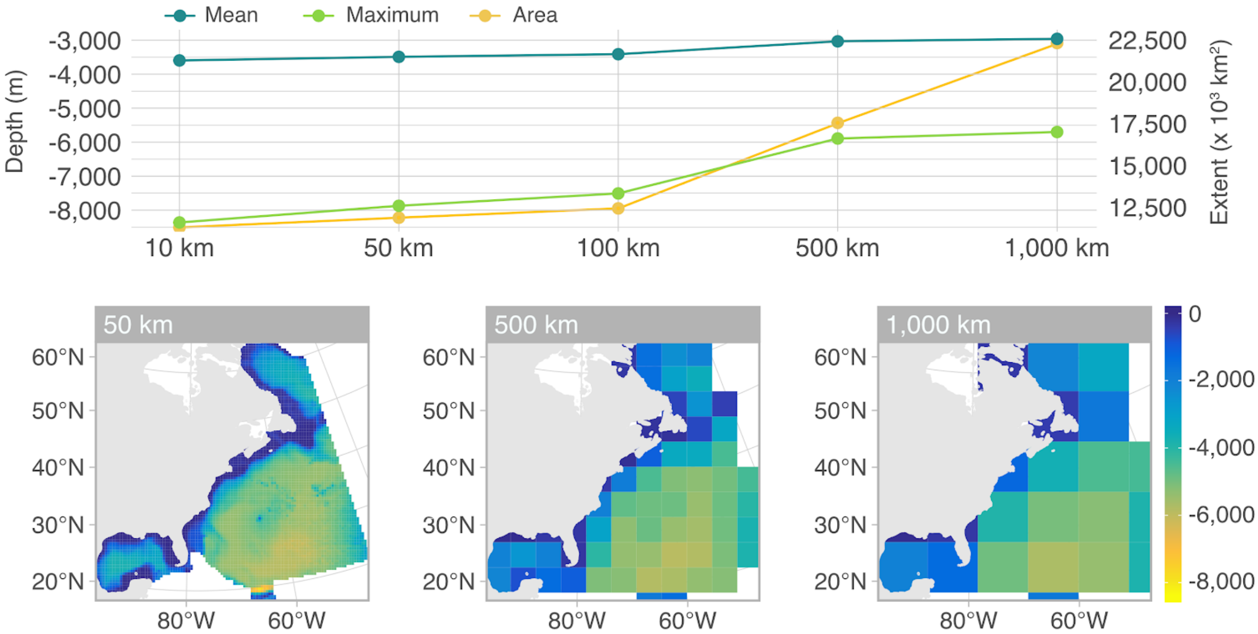

Figure 6: Effects of upscaling a bathymetric grid of the U.S. Navy's Atlantic Fleet Training and Testing (AFTT) area, in the Northwest Atlantic. The top panel shows the mean and maximum depth as well as the surface area for rasters at different resolutions. The bottom panel shows three example maps. The range of depth values shrinks when the original raster, available at 10 km resolution, is resampled to coarser grains (50, 100, 500, and 1000 km).

Similarly, temporal matching is important for extrapolating models through time (Guisan et al. 2017), yet ecologists have been unscrupulous in considering the influence of temporal resolution on model predictions, at least until recently (Kearney et al. 2012; Fernandez et al. 2017; Mannocci et al. 2017a). Highly mobile animals like cetaceans interact with a range of dynamic and ephemeral oceanographic processes, and may respond to daily, weekly or seasonal climate and weather patterns more acutely than to long-term trends in some contexts, or vice-versa. Many variables commonly used in DSMs also show significant variation over time scales ranging from seconds to decades, making informed choices of environmental data contemporaneous to animal presence, abundance or movement (e.g. daily, weekly), versus averaged products (monthly, seasonal, climatological) all the more crucial (Scales et al. 2017).

Ultimately, no single model can be expected to work flawlessly for all taxa, in all areas, and at all times (Jarnevich et al. 2015; Qiao et al. 2015). It is worth noting, therefore, that extrapolation is also influenced by model choice, model complexity, and model tuning (Buisson et al. 2010; Anderson & Gonzalez 2011; Merow et al. 2014). Numerous studies have attempted to benchmark the performance of different modelling approaches under a range of parameterisation scenarios, with mostly inconsistent results (Meynard & Quinn 2007; Syphard & Franklin 2009; Beaumont et al. 2016; Shabani et al. 2016). A practical dilemma is that several model structures or formulations may fit the reference data equally well (an issue known as ‘equifinality’ or ‘non-identifiability’) (Bucklin et al. 2015), yet lead to diverging predictions in the target system (Fygenson 2008; Dormann et al. 2012; Domisch et al. 2013). Simpler, more parsimonious models are often preferred to maximise ecological realism and interpretability. However, they also threaten to ignore key processes and, with insufficient flexibility to describe ecological relationships, can extrapolate poorly (Thuiller et al. 2004; Evans et al. 2013). By contrast, extrapolation is naturally more pervasive when the number of covariates increases (Authier et al. 2017), and more complex and flexible models risk overfitting - i.e. capturing data idiosyncrasies and noise at the expense of true signals - such that they will not generalise to conditions other than those encountered during calibration (Bell & Schlaepfer 2016). While this has led some authors to advocate for models of intermediate complexity (Moreno-Amat et al. 2015), building simple and complex models may ultimately serve different purposes, and a preference for one approach over another may be equally justifiable depending on the specific context of a given study (see Merow et al. 2014 for a detailed discussion). For example, an ‘overfitting’ model may be more desirable for identifying areas suitable for the re-introduction of rare captive-bred species, whereas simpler models may be better equipped to guide searches for remnant populations of possibly extinct species (Escobar et al. 2018). In any case, it is clear that predictions from correlative models are often only as good as our knowledge of the mechanisms and feedbacks that underlie ecological patterns (Miller et al. 2004). Successful models are therefore likely to be those based on relatively simple relationships grounded in mechanisms that are well understood (Yates et al. 2018; Bouchet et al. 2019).

2.4 Some solutions

Despite some arguments that extrapolation should only be justified as an exploratory exercise (Boyd et al. 2010), untested predictions derived from the best available science are still viewed by many as a more desirable outcome than proceeding blindly (Miller et al. 2004). In particular, projecting models into novel contexts remains a practical necessity in many ecological risk assessments (Forbes & Calow 2002), and cannot be circumvented when seeking answers to questions relating to non-analogue climate scenarios or species' range expansions (Merow et al. 2014).

Three main strategies have therefore been proposed to deal with extrapolation (but see Elith & Leathwick 2009 for additional solutions), namely: avoidance, mitigation, and diagnosis (Owens et al. 2013; Sequeira et al. 2018a).

- **Avoidance:** Truncating model predictions (**Fig. 7A**) by discarding or masking any that are produced outside the space of the reference data offers a simple and effective way of avoiding extrapolation. There have been suggestions that extrapolations may be deemed negligible if model predictions are not made beyond one-tenth of the sampled covariate range (Dormann 2007). However, this is only a generic guideline that is unlikely to provide consistent results in most contexts.

- **Mitigation:** Clamping (or 'bounding'), i.e. holding predictions constant at the marginal value obtained in the calibration area (**Fig. 7B**), can help alleviate potential extrapolation errors and is the default setting in some software packages such as MaxEnt (Stohlgren et al. 2011; Merow et al. 2013). Although this is a conservative approach, clamping at high values may lead to density estimates that are inflated unrealistically when extrapolating (Guevara et al. 2018). A more pragmatic solution would be to reduce the likelihood of encountering novel combinations of environmental conditions in the first place, for example by sampling the complete breadth of a species' geographic range given its dispersal abilities and limitations, wherever possible (Thuiller et al. 2004). With an average range of 52 million km^2 across taxa, this is impossible for most marine mammals (Pompa et al. 2011).

- **Diagnosis:** When extrapolation is unconstrained, response curves are extended based on trends observed within reference conditions and some assumptions about the niche (**Fig. 7C**) (Mannocci et al. 2017b). This approach can be advantageous insofar as it does not preclude ecological inference outside the sampled conditions, i.e. when and where it may be most urgently needed (Sequeira et al. 2018a). However, its validity depends on the directionality of response curves at the edge of the calibration domain; increasing curves may lead to unrealistic results (Guevara et al. 2018), particularly if extrapolation is performed on a log-transformed scale (**Fig. 5**). As a result, rigorous assessments of the extent and magnitude of extrapolation are critical to supporting appropriate interpretations of model predictions in light of their inherent uncertainty (e.g. maps of "ignorance" depicting where predictions may be questionable; Rocchini et al. 2011). Because independent target data are often lacking - preventing direct model validation - such assessments usually rely on evaluations of the level of environmental similarity between reference and target systems, as a proxy for extrapolation (see section **2.5**) (Elith & Leathwick 2009; Werkowska et al. 2017).

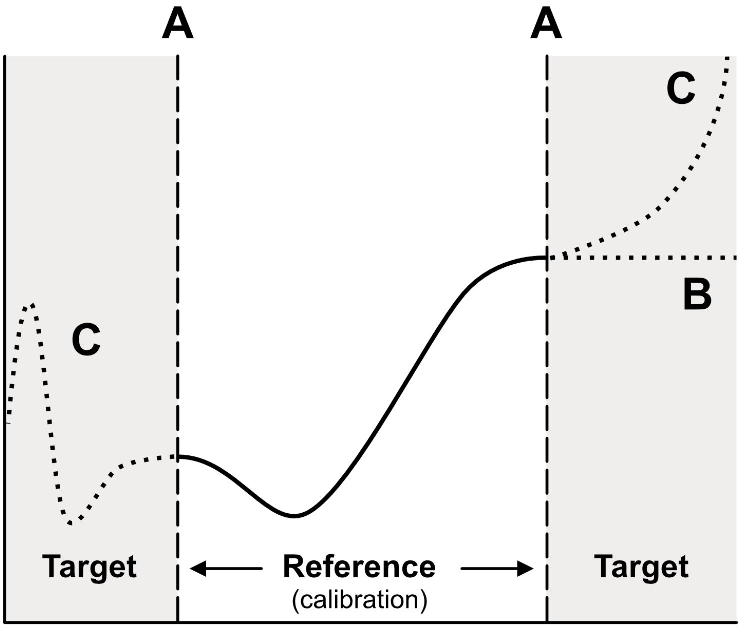

Figure 7: Three approaches to dealing with extrapolation in predictive ecological models. **(A)** Truncation: Model predictions made outside the calibration domain (i.e. the grey area) are discarded. **(B)** Clamping: Model predictions are capped at the edge value encountered during calibration. **(C)** Extrapolation is unconstrained and must be appropriately evaluated. Figure adapted from Owens et al. (2013).

2.5 Extrapolation metrics

Several quantitative extrapolation diagnostics have been proposed in recent years (**Table 2**), yet metric selection is rarely justified in published studies, with little consensus on which index is best suited to a given scenario, and limited consideration of how results may ultimately be sensitive to metric choice (Grenier et al. 2013). This lack of clarity is alarming given the prominent role that extrapolated models play in addressing socio-economic and ecological issues in areas such as infectious disease mitigation, agricultural pest control, or endangered species conservation (Acevedo et al. 2014; Escobar et al. 2018).

Table 2: Summary of the main extrapolation diagnostics used in ecological models (listed in chronological order of publication). Recommended metrics are marked with an asterisk (see main text for rationale). Associated references are as follows: %N (King & Zeng 2007); SED (Williams et al. 2007); MESS (Elith et al. 2010); PURV (Rödder & Engler 2012); Inflated response curves (Zurell et al. 2012); MOP (Owens et al. 2013), ExDet (Mesgaran et al. 2014); gIVH (Conn et al. 2015a); σ dissimilarity (Mahony et al. 2017); E-space I and II (Escobar et al. 2018).

Metric	Caveats and limitations
Percentage of Data Nearby (%N) *	Relies on a subjective definition of neighbourhood (i.e. the radius distance from reference points).
Standardised Euclidean Distance (SED)	Susceptible to variance inflation due to covariate correlations. Does not account for the effect of dimensionality (i.e. number of covariates).
Multivariate Environmental Similarity Surface (MESS)	Only considers univariate extrapolation outside the univariate range of individual covariates. Uses a rectilinear technique for extrapolation detection, despite environmental envelopes often being obliquely elliptic. Environmental similarity measured relative to the most dissimilar covariate only, such that two prediction points may receive the same value based on different covariates.
Prediction Uncertainty assessments using Residual Variation (PURV)	Only assesses changes in correlation structures between predictors (aka. combinatorial extrapolation), based on a conservative assumption of linearity. May be unreliable when inter-predictor relationships are complex and nonlinear.
Inflated Response Curves and Environmental Overlap ('gap') masks	Entails dimensionality reduction (via Latin hypercube sampling) for large numbers of covariates, incurring some data loss. Combinatorial extrapolation identified using a binning approach, with some degree of subjectivity associated with bin choice. Output is binary and does not measure the magnitude of environmental 'novelty'.
Mobility-Oriented Parity (MOP)	Only considers univariate extrapolation, similarly to MESS.
Extrapolation Detection (ExDet) *	Combinatorial extrapolation only supports linearly correlated, quantitative variables, similarly to PURV.
Generalised Independent Variable Hull (gIVH)	Dependent on data quality. If prediction variance (e.g. coefficient of variation) for the observed data is high (e.g. in a DSM from surveys run in 'Beaufort 8 and in the dark'), then extrapolation may be not be detected.
Sigma dissimilarity (σ)	Hinges on the interannual environmental variability of the location of interest, but ignores that of candidate analogs. Therefore, likely underestimates novelty relative to methods that account for analog environmental variability.
Environmental Space Indices (E-space I and II)	Evaluations of environmental novelty constrained to three-dimensional space based on the axes of a principal component analysis of predictor covariates. Incurs data loss due to dimensionality reduction.

Extrapolation detection methods are typically *extrinsic* (i.e. independent of the model itself) (Grenier et al. 2013), with the most common being to interpret predictions relative to the numerical range of each covariate entering the model. Predictions at covariate values outside the range of observed data are labelled as ‘extrapolations’, and those within the range are denoted ‘interpolations’ (Qiao et al. 2019) (**Fig. 8A**). Many studies have shown that predictive accuracy is impaired when a model is extrapolated to new sites or time periods (Torres et al. 2015; Roach et al. 2017; Sequeira et al. 2018b), making this dichotomy appealing for identifying subsets of predictions that can reasonably be expected to be less reliable, all things being equal (Randin et al. 2006; Heikkinen et al. 2012).

Covariate values, however, are rarely distributed homogeneously in covariate space (**Fig. 8A**). Even predictions classed as ‘interpolations’ (light yellow area in **Fig. 8A**) may include novel combinations of values not encountered in the original sample (Mesgaran et al. 2014). A more nuanced typology of extrapolation is required that recognises the reference points as occupying a discrete volume (i.e. envelope) within the hyperspace of modelled covariates. The simplest delineation of this envelope is a hyperpolyhedron (i.e. convex hull) or an ellipsoid that encompasses the most extreme observations of each covariate (King & Zeng 2007; García-López & Allué 2013).

It follows that three types of extrapolation can be identified (**Fig. 8B**):

- **Univariate** extrapolation, which identifies out-of-range values for any given covariate. Also known as mathematical, strict, novel or Type 1 extrapolation (dark blue in **Fig. 8B**).
- **Combinatorial** extrapolation, which detects novel combinations of values encountered within the univariate range of reference covariates. Also known as multivariate, novel-combination, or Type 2 extrapolation (dark yellow in **Fig. 8B**).
- **Geographic (and/or temporal)** extrapolation, which corresponds to conditions analogous to those characterising the reference data, although these may occur in a different region in space or a past/future period in time. Equivalent to interpolation (light red in **Fig. 8B**).

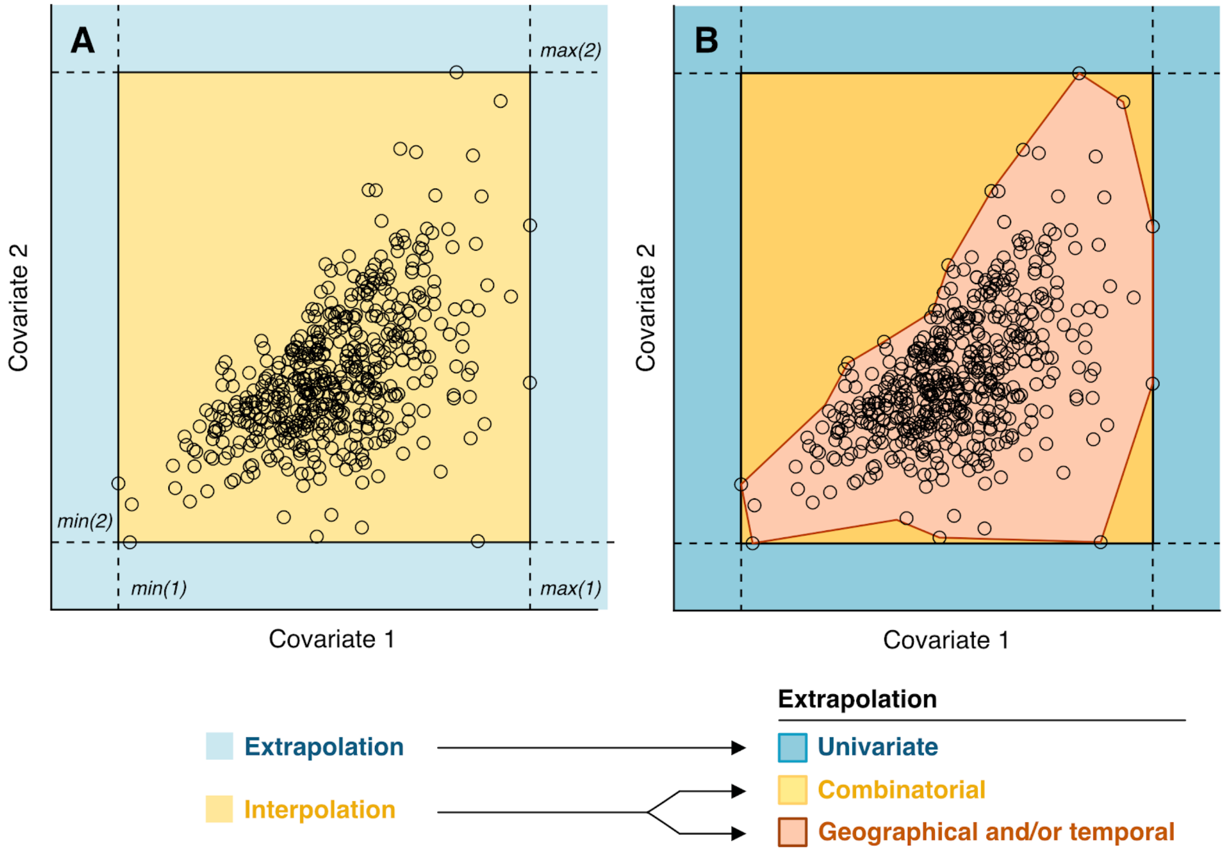

Figure 8: Typology of environmental extrapolation, with black circles denoting reference samples. **(A)** Simple binary classification defined in the bivariate space of two hypothetical environmental covariates. Interpolation here occurs when points fall within the rectangle defined by the minimum and maximum values of individual covariates (light yellow). Extrapolation takes place outside that rectangle (light blue). **(B)** Refined classification that also considers novel combinations of covariates (dark yellow), as per Mesgaran et al. (2014). By contrast, out-of-range predictions are now termed 'univariate' extrapolations. Any points within the envelope (red outline) of the sampled data correspond to conditions analogous to those found in the reference system, and are termed 'Geographical/temporal extrapolation' if found in a different region or time slice.

While this taxonomy is an improvement over the binary classification shown in **Fig. 8A**, two fundamental issues remain. Firstly, it is still categorical and fails to distinguish models that extrapolate with similar frequency (i.e. extent) but different intensity (i.e. magnitude). For instance, two models developed from data spanning a 10-20°C interval could be used to make an equal number of predictions outside this range (e.g. five values each), yet one may extrapolate to 21°C only, while the other could stretch to 100°C (Escobar et al. 2018). In this scenario, it is rational to expect that the predictions of the former ought to be more reliable, as they are closer to the sampled environmental space (**Fig. 9A**). Secondly, it is possible for predictions made in analogue conditions to fall within sparsely sampled regions of the reference space; or conversely, for two target points reflecting an equal degree of extrapolation *stricto sensu* to contain very different amounts of reference data in their vicinity. An example of this is shown in **Fig. 9B**, where three target points X_1, X_2, and X_3, are located at equal distances to the envelope of the reference data.

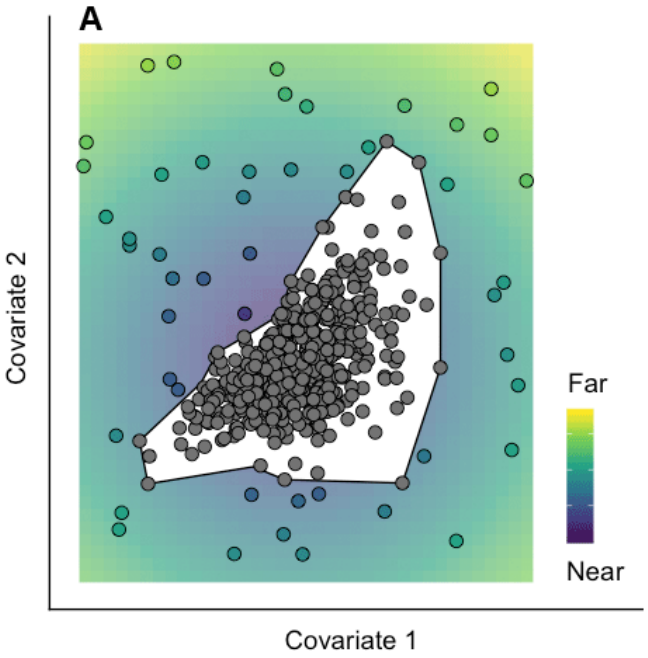

Figure 9: Conceptual representation of two key extrapolation metrics. **(A)** Distance from the envelope (black polygon) of the reference data (grey circles). A target point located far outside the sampled environmental space (e.g. falling in the yellower areas) is more dissimilar and therefore 'more of an extrapolation' than one closer to it (e.g. falling in the bluer areas). **(B)** Neighbourhood (or 'percentage of data nearby'). Owing to the complex shape of the reference data cloud in multivariate space, the amount of sample information available to 'inform' predictions made at target points can vary considerably. For instance, contrast the proportion of reference data points (in green) contained within comparable radii of prediction points X_1 and X_3.

However, given the shape of the data cloud in multivariate space, it is apparent that predictions made at target point X_1 will be far better 'informed' than those made at either X_2 or X_3, since it is adjacent to a larger cluster of sample data. Ideally, extrapolation assessments should explicitly capture these two components of **distance** and **neighbourhood** (**Fig. 9**). Expressing extrapolation as a continuous variable gives a more nuanced view of the issue (Radeloff et al. 2015). We therefore propose that two of the metrics listed in **Table 2** should be used as standard tools for evaluating extrapolation in abundance models developed from cetacean line transect data, namely the Extrapolation Detection (**ExDet**) tool developed by Mesgaran et al. (2014) and the percentage of data nearby (**%N**) put forward by King and Zeng (2007).

ExDet harnesses the properties of a scale-invariant measure of multivariate outliers, the Mahalanobis distance, to characterise the degree of novelty/similarity between reference and target domains. Doing so gives ExDet a number of advantages (Farber & Kadmon 2003):

- It is relevant to both orthogonal and correlated covariates, and can accommodate the latter even if they exhibit heterogeneous variances. Mathematically, the Mahalanobis distance reduces to a standardised Euclidean distance when the covariance between variables approaches zero (i.e. variables are orthogonal to each other) (Mahony et al. 2017).
- It accounts for different dispersions between covariates through standardisation.
- It is robust to departures from multivariate normality.
- It allows a natural definition of the most influential covariates (MIC), i.e. those that make the largest contribution to extrapolation in the target system.
- It has a clear theoretical basis that aligns with the principle of central tendency as expressed in niche theory (Whittaker 1975), which suggests that species' survival is maximised in optimal conditions and reduces to zero outside environmental tolerance limits.

Furthermore, ExDet simultaneously accounts for both univariate and combinatorial extrapolation, yielding a more comprehensive picture of extrapolation that is lacking from other metrics or otherwise difficult to obtain in a manner functional for model end-users (Mesgaran et al. 2014). Addressing combinatorial extrapolation is especially important as model predictions may only be reliable where collinearity patterns among covariates remain stable (Rödder & Engler 2012). Note that, by design, ExDet only detects combinatorial extrapolation within the rectilinear envelope of input covariates (**Fig. 8B**), however extensions to the framework have recently been proposed to broaden its applicability (Muthoni et al. 2017). Note also that Mahalanobis distances vary as a function of the number of selected covariates. The effect of covariate dimensionality on ExDet outputs is therefore a critical consideration for their correct interpretation (Mahony et al. 2017). Small covariate sets should carry lower risk of false positives (akin to Type I inference errors), but at the cost of potentially higher rates of false negatives (akin to Type II errors) (Mahony et al. 2017). In the absence of abundance data in the target system, it is hard to find an objective basis for choosing a specific covariate set over another, other than purely through ecological reasoning. That said, it can be shown the distribution of Mahalanobis distances for multivariate normal data is approximated by a χ^2 distribution with $n-1$ degrees of freedom, where n equals the number of covariates/dimensions (Clark et al. 1993; Farber & Kadmon 2003). It follows that Mahalanobis distances can be expressed probabilistically as percentiles of the χ^2 distribution (Mahony et al. 2017), allowing a more transparent and meaningful interpretation of the significance of extrapolation.

By contrast, %N uses the Gower's distance (Faith et al. 1987) to quantify the proportion of reference data lying within a given radius of any prediction point (Stoll et al. 2005), an often overlooked dimension of extrapolation. Typically, the geometric variability present in the reference sample acts as a rule of thumb threshold, such that prediction points are considered ‘nearby’ if they sit within one geometric mean Gower’s distance of the data (the mean value being calculated between all pairs of reference points; King & Zeng 2007). %N has the benefit of being applicable to both quantitative and qualitative variables, and has been used with success in previous studies of cetacean populations (Virgili et al. 2017; Mannocci et al. 2018; García-Barón et al. 2019).

Our recommendation for these metrics is motivated by the fact that they fulfil most of Grenier et al. (2013)’s criteria for metric selection, including quantifying extrapolation on unambiguous continuous scales, being conceptually straightforward, and being easily implemented in open-source software packages such as R at minimal computational cost (see section **3**). When combined, ExDet and %N help capture the two important and complementary dimensions of environmental analogy and availability (sensu Guisan et al. 2017), and may allow practitioners to be more objective and efficient at discriminating between uncertain (i.e. high extrapolation, limited environmental analogy) and trustworthy (i.e. low extrapolation, high analogy) predictions (Escobar et al. 2018). Critically, neither requires any model fitting; the definition of an environmental extrapolation is thus model independent (García-Barón et al. 2019).

3. Software

This report is accompanied by a dedicated R package, `dsmextra`, which is fully described in Bouchet et al. (2020). The package website (https://densitymodelling.github.io/dsmextra/) includes a tutorial vignette covering practical examples of extrapolation assessments for both sperm whale (*Physeter macrocephalus*) and beaked whale (*Ziphiidae spp*) DSMs in the popular software R. The data used in the case studies come from shipboard and aerial line transect surveys undertaken across the North Atlantic and Gulf of Mexico, and are fully described in Roberts et al. (2016) and Mannocci et al. (2017).

`dsmextra` comprises five key functions:

- `compute_extrapolation`: This function calls `ExDet` and returns results in both data.frame and raster formats.
- `compute_nearby`: This is a wrapper around `whatif` and `whatif.opt` that quantifies the proportion of reference points located in the vicinity of each target point in multivariate space, as an additional metric of extrapolation. See King and Zeng (2007) for details.
- `compare_covariates`: This is a wrapper around `compute_extrapolation` that can be used to assess extrapolation for different combinations of covariates, as a means of informing covariate selection during model development.
- `map_extrapolation`: This function supports the visual assessment of extrapolation by generating interactive html maps of the outputs from `compute_extrapolation`.
- `extrapolation_analysis`: This function allows a full assessment of extrapolation (i.e. calculations, summary, and visualisation) to be conducted in one single run, by combining calls to `compute_extrapolation`, `summarise_extrapolation`, and `map_extrapolation`.

Some of these rely on internal functions:

- `ExDet`: An adaptation of the `ecospat.climan` function from the `ecospat` package (formerly `ecospat.exdet` in previous releases of the package). It is used to assess the degree of environmental similarity between a reference and a target system, as described in Mesgaran et al. (2014), with the added functionality of identifying the most influential covariate(s) - MIC - i.e. contributing most to departures from reference conditions.
- `whatif.opt`: An adaptation of the `whatif` function from the `WhatIf` package (Stoll, King, and Zeng 2005), modified to run on large datasets via matrix partitioning.
- `summarise_extrapolation`: Function to summarise extrapolation results in tabular form.

See Bouchet et al. (2020) and the package help files for further details.

4. Outlook and recommendations

Pressing needs to tackle the challenges posed by climate warming, habitat loss, and species extinctions have spurred strong demands for ecological models that can help elucidate wildlife abundance and distribution patterns across a variety of scales, and to foresee the responses of biodiversity to multiple drivers of change (Coreau et al. 2009; Mouquet et al. 2015; Maris et al. 2018). However, despite sustained efforts to survey the Earth's' biomes over the last decades (Costello et al. 2010), detailed occurrence or density maps are still unavailable for most taxa (Green et al. 2005). In the wake of a worldwide economic crisis, cuts in conservation spending are also forcing agencies responsible for biological data collection to operate on shoestring budgets, limiting the scope of further monitoring and field sampling to smaller areas, shorter and more irregular time spans, and cheaper assessment methods (Borja & Elliott 2013). As anthropogenic impacts on ecosystems continue to accelerate, there is hence increasing appetite for translating sporadic ecological understanding accumulated at local or regional levels into broad-scale insights that can facilitate strategies to manage and adapt to the effects of global change (Heffernan et al. 2014). This makes extrapolation a pivotal – if not imperative – component of research agendas in applied ecology (Colwell & Coddington 1994; Clark et al. 2001), particularly within the marine arena (e.g. Redfern et al. 2017; Péron et al. 2018; Sequeira et al. 2018a).

There is no doubt that by extrapolating we are using models in risky ways, pushing to formalise processes which have not been documented or validated with any empirical data (Williams & Jackson 2007; Elith & Leathwick 2009). The potential for errors to arise during extrapolation is therefore non-negligible (Fitzpatrick et al. 2007; Richmond et al. 2010), and the predictive performance of many types of statistical algorithms has indeed been shown to decrease when they are being projected into out-of-sample conditions (e.g. applied to a different geographic area or future time period) (e.g. Dobrowski et al. 2011; Torres et al. 2015; Sequeira et al. 2016, 2018b; Roach et al. 2017). Worryingly, general awareness of extrapolation and its implications for predictive inference seems to be lacking within many disciplines of science (Enserink 2001), wrongly encouraging practitioners to take extrapolated predictions at face value, irrespective of their uncertainties and biases (Sutherst & Bourne 2009; Beale & Lennon 2012). In conservation planning in particular, the need for immediate solutions to data deficiency often overrides caution in extrapolation, such that model predictions are tacitly treated as reliable (Rocchini et al. 2011; Sequeira et al. 2018a). Concerns about these behaviours, and ongoing debate surrounding the inherent predictability of nature (for instance, contrast Beckage et al. (2011) with Mouquet et al. (2015)), have fuelled a certain degree of pessimism about extrapolation, prompting some authors to regard it as a form of 'statistical felony' that should only be warranted purely for the purposes of data exploration (Boyd et al. 2010).

We adopt a more optimistic viewpoint; one that acknowledges predictions as a useful way of testing and demonstrating ecological understanding (Houlahan et al. 2017), and that recognises accurate forecasting as a hallmark of successful science (Evans et al. 2012). We argue that, when exercised with due diligence, extrapolation can be a powerful driver of scientific conjecture and discovery (Coreau et al. 2009), such that methods supporting the projection of models into novel conditions are paramount to catalysing future advances in fields like conservation planning, agriculture, engineering or epidemiology (Acevedo et al. 2014). One of the greatest obstacles to extrapolating well-fitted DSMs to novel conditions, of course, is the lack of target data with which to validate predictions in many information-poor ecosystems (e.g. Redfern et al. 2017). Counter-intuitively, extrapolation is both a consequence of, and a solution to, data deficiency in this context. By projecting models, we can generate null hypotheses against which new data can subsequently be checked (as and when they become available), allowing extrapolation to serve as an instrument of learning that fosters long-term improvements in predictive ability (Petchey et al. 2015; Pennekamp et al. 2017). Extrapolation can also be strategically applied to the formulation of survey designs, and one could easily think of augmenting a sampling scheme with a number of sites expected to exhibit high prediction variance (Conn et al. 2015a), or simply guiding survey efforts to those areas with higher probabilities of species occurrence or abundance (Bourke et al. 2012; Mannocci et al. 2018).

Ultimately, embracing the potential of extrapolation in ecology hinges on raising awareness of its possible shortcomings (Gillman 2009) and harmonising approaches to its detection and reporting (Sequeira et al. 2018a). Fortunately, a number of useful ideas have recently been emerging for probing models and predictions, empowering end-users with a refined understanding of model behaviour in novel domains (Zurell et al. 2012). The main objective of this report was to summarise the computational tools currently available for identifying, quantifying, and visualising extrapolation in novel environmental space, providing a simple and intuitive protocol for determining the safest way to proceed outside the sample bounds (Elith et al. 2010). Developing more rigorous extrapolation practice is critical to better informing policy makers and the public (Pennekamp et al. 2017). We proposed that two complementary metrics, ExDet and %N, could be used to support a standard approach to extrapolation assessments in cetacean DSMs, although their applicability also extends to other organisms and study systems. Put together, ExDet and %N provide a holistic, model-agnostic appraisal of extrapolation that accounts for various types of departures from reference conditions, and enables the geographic and temporal distribution of extrapolation to be easily displayed on a map. The latter is of particular importance for alleviating skepticism in conservation decisions (Uribe-Rivera et al. 2017; Qiao et al. 2019). ExDet and %N also make assessments of relative prediction reliability possible. Based on these metrics, the more trustworthy predictions will be those associated with a lower percentage of extrapolation and a higher percentage of neighbourhood. Reliability, thus defined (**Fig. 10**), reflects how predictions are informed by actual data vs. modelled inferences

(García-Barón et al. 2019), such that one can place more confidence in a prediction that is informed by a lot of data than in a prediction that is not, although both may turn out to be correct if the model used for prediction captures accurately the underlying relationships between the covariates and the response variable (cetacean abundance in this case) (García-Barón et al. 2019).

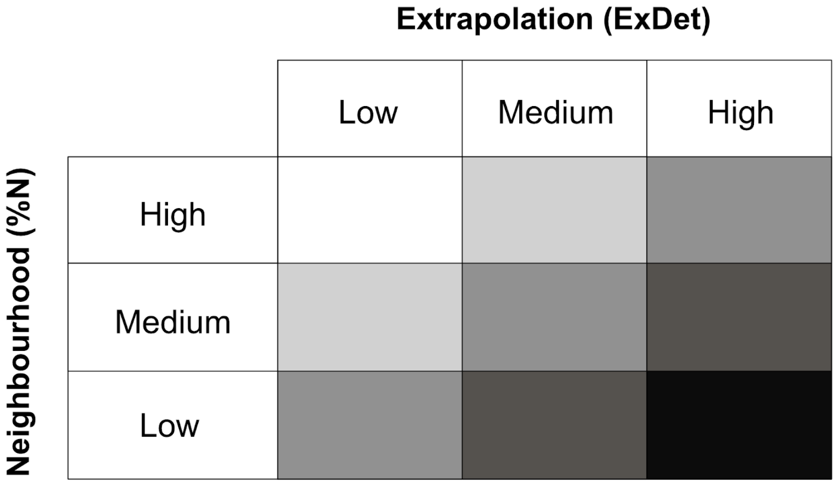

Figure 10: Simple matrix for interpreting extrapolation assessments based on the combination of ExDet and %N. The shading of each indicates the degree of reliability of each extrapolation scenario, from black (least reliable) to white (most reliable).

Choosing a threshold for classifying low and high values of ExDet and %N is not trivial. A simple rule could be to rank points according to their position relative to the median value obtained in the target system. However, this approach is strongly region-specific and unlikely to yield consistent results across studies and taxonomic groups. Sensitivity analyses are valuable for exploring the effects of such arbitrary decisions in ecology (Cariboni et al. 2007), and may be a useful alternative here, by determining how abundance estimates fluctuate in response to changes in the extent and magnitude of extrapolation. Relevant methods will be explored in a revised version of this report and incorporated in an updated release of the R code.

The main goal of extrapolation is to deliver actionable information about the states and trajectories of ecological systems. As such, it does not so much matter how predictions are obtained, so long as they can prove useful (Pennekamp et al. 2017). Petchey et al. (2015) proposed the concept of ‘forecast horizons’ to define the limit(s) beyond which sufficiently useful predictions can no longer be made in any given dimension (e.g. space, time, phylogeny, environment). Different stakeholders and model end-users (e.g. spatial planners, resource managers, government scientists, military bodies) undoubtedly have different opinions as to what constitutes ‘good enough’, and a significant challenge therefore lies in reconciling their perspectives and specific forecast horizons to provide practical guidelines that are intelligible and admissible to all (Yates et al. 2018). Critical to this is stronger transparency around the purpose of extrapolated models. Ideally, the first step in any extrapolation should thus be an explicit statement of research objectives, framed (wherever possible) in a prior understanding of the expected relationships (empirical and/or mechanistic) between response and predictor variables of interest (e.g. based on pilot studies or reviews of the published literature) (Miller et al. 2004). This is an important exercise, which not only clarifies the scope of model projections (what is being predicted, and why) (Petchey et al. 2015), but also helps to identify the processes that are prone to affect animal abundance within reference and target extents, to recognise likely sources of errors and uncertainty, and to justify the selection of meaningful explanatory covariates. Extrapolation always requires that predictions be checked for biological plausibility (Merow et al. 2014), yet ecologists are often too tempted to include numerous routine, widely available predictors with the expectation that the true ecological drivers among them will naturally come out in the wash (Guisan et al. 2017; Strong & Elliott 2017). However, the more covariates enter models, the more combinations of their values there can be, and the higher the risk of detecting false novelty (Type I errors) (Mahony et al. 2017). Failure to filter variables based on a well-founded biological justification may thus lead to unreasonable predictions of species' responses to novel conditions (Petitpierre et al. 2017). Our R code includes tools for exploring combinations of variables and assisting with covariate choice.

5. Future directions

Rather than an end point, extrapolation should be best viewed as part of a cycle that entails the application and subsequent revision of what is known (Miller et al. 2004). By assessing conditions under which models consistently fail or succeed in extrapolating, ecologists are likely to gain a more in-depth understanding of ecological patterns and their underlying drivers (Yates et al. 2018). It is our hope that this report can serve as a platform for catalysing such assessments going forward.

That said, a number of areas deserve further attention, including:

- Finding better methods of formally integrating expert knowledge in extrapolation, likely through Bayesian frameworks (Kuhnert et al. 2010; Merow et al. 2017; Niamir et al. 2019).
- Considering the role of model structure on the quantification of extrapolation, i.e. *intrinsic* extrapolation. For instance, edge effects tend to be apparent in predictions derived from conditionally autoregressive models (Conn et al. 2015b).
- Developing ways to breathe more mechanism into abundance models (Bouchet et al. 2019), for example by assimilating data from process-based studies or models during statistical formulation, building hybrid/coupled models where the output of a mechanistic model is used as the input to a correlative one, or simply by comparing predictions with process‑based models to learn from where do or do not agree (Franklin 2013).
- Exploring the effects of seascape patches and mosaics, as many extrapolation errors arise from the failure to consider their nature and magnitude (Miller et al. 2004).
- Accounting for biotic interactions in predictive models such as DSMs and quantifying their impacts on extrapolations under various scenarios of associations between species (Bateman et al. 2012; Leach et al. 2016).
- Actively incorporating species demography and population dynamics, by accounting for migration, dispersal and reproductive rates, for instance through dynamic range models and integrated hierarchical models (Forbes et al. 2008; Franklin 2010b; Schurr et al. 2012).
- Combining extrapolation assessments from different models within ensemble frameworks and for temporally dynamic covariates (e.g. monthly predictions over a year).

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