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Review

# Outstanding Challenges in the Transferability of Ecological Models

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**Predictive models are central to many scientific disciplines and vital for informing management in a rapidly changing world. However, limited understanding of the accuracy and precision of models transferred to novel conditions (their 'transferability') undermines confidence in their predictions. Here, 50 experts identified priority knowledge gaps which, if filled, will most improve model transfers. These are summarized into six technical and six fundamental challenges, which underlie the combined need to intensify research on the determinants of ecological predictability, including species traits and data quality, and develop best practices for transferring models. Of high importance is the identification of a widely applicable set of transferability metrics, with appropriate tools to quantify the sources and impacts of prediction uncertainty under novel conditions.**

## Highlights

Models transferred to novel conditions could provide predictions in data-poor scenarios, contributing to more informed management decisions.

The determinants of ecological predictability are, however, still insufficiently understood.

Predictions from transferred ecological models are affected by species' traits, sampling biases, biotic interactions, nonstationarity, and the degree of environmental dissimilarity between reference and target systems.

We synthesize six technical and six fundamental challenges that, if resolved, will catalyze practical and conceptual advances in model transfers.

We propose that the most immediate obstacle to improving understanding lies in the absence of a widely applicable set of metrics for assessing transferability, and that encouraging the development of models grounded in well-established mechanisms offers the most immediate way of improving transferability.

## Predicting the Unknown

Predictions facilitate the formulation of quantitative, testable hypotheses that can be refined and validated empirically [1]. Predictive models have thus become ubiquitous in numerous scientific disciplines, including ecology [2], where they provide means for mapping species distributions, explaining population trends, or quantifying the risks of biological invasions and disease outbreaks (e.g., [3,4]). The practical value of predictive models in supporting policy and decision making has therefore grown rapidly (Box 1) [5]. With that has come an increasing desire to **predict** (see Glossary) the state of ecological features (e.g., species, habitats) and our likely impacts upon them [5], prompting a shift from **explanatory** models to **anticipatory predictions** [2]. However, in many situations, severe data deficiencies preclude the development of specific models, and the collection of new data can be prohibitively costly or simply impossible [6]. It is in this context that interest in transferable models (i.e., those that can be legitimately projected beyond the spatial and temporal bounds of their underlying data [7]) has grown.

Transferred models must balance the tradeoff between estimation and prediction bias and variance (homogenization versus nontransferability, *sensu* [8]). Ultimately, models that can

## Box 1. Why Transfer Models in the First Place?

Ecological models are extensively and increasingly used in support of environmental policy and decision making [77]. The process of transferring models typically stems from the need to support resource management in the face of pervasive data deficiencies, limited research funding, and accelerating global change [5]. Spatial transfers have been used to guide the design of protected areas, search for species on the brink of extinction, inform species relocations or reintroductions, outline hotspots of invasive pests, design field sampling campaigns, and assist the regulation of human activities (e.g., [78,79]). For instance, cetacean density models developed off the east coast of the United States were recently extrapolated throughout the western North Atlantic high seas to assist the management of potentially harmful sonar exercises performed by the military [80]. Similarly, projections of Asian tiger mosquito (*Aedes albopictus*) distribution models onto all continents helped identify areas at greatest risk of invasion, with important implications for human health [81]. Temporal transfers have largely been applied to forecast species' responses to climate warming, retrospectively describe pristine population states, characterize evolutionary patterns of speciation, quantify the repercussions of land use changes, or estimate future ecosystem dynamics (e.g., [68,72,82]). Despite being difficult to quantify, the societal and economic gains from transferring models can be substantial, and are most readily illustrated by the mitigation of costs associated with invasive species [83]. For instance, the establishment of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes region of North America has led to $20–100 million in annual mitigation expenditure, with additional, unquantified nonmarket costs ensuing from the loss of biodiversity and ecosystem services [5]. Transferred models accurately predicted the establishment of the zebra mussel 5 years before it was actually discovered in the region, however model predictions were not used to take preventative action, illustrating that developing a transferable model is only the start of the road to informing decision makers (see Outstanding Questions). Ultimately, the widespread need to make proactive management decisions in data-poor situations drives the need to improve our understanding of model transferability. This goal fundamentally requires better transferability metrics and estimates of prediction uncertainty, which can assist in selecting the most consistent and effective management options while avoiding unanticipated outcomes [84].

simultaneously achieve high accuracy and precision, even when predicting into novel contexts, will provide maximum utility for decision making [9]. To date, however, tests of **transferability** across taxa and geographic locations have failed to demonstrate consistent patterns (Figure 1), and a general approach to developing transferable models remains elusive (but see [6,10]). Here, we outline challenges that, if addressed, will improve the harmonization, uptake, and application of model transfers in ecology. We argue that moving the field of model of transferability forward requires a two-pronged approach focused on: (i) investing in fundamental research aimed at enhancing predictability, and (ii) establishing technical standards for assessing transferability.

## Defining the Challenges

We first identified challenges using a modified Delphi technique [11] (see the supplementary information online), and then divided them into those that reflected conceptual obstacles ('fundamental challenges'), and those related to best practices ('technical challenges'). Acknowledging significant overlap and linkages between these challenges (Figure 2), we explore each separately below. Attempts to understand and enhance transferability face many of the same hurdles as ecological modeling generally (e.g., data quality, stochasticity), and adhering to best practice recommendations (e.g., [12,13]) is thus imperative. We do not focus on these well-established standards, but concentrate on the additional challenges posed by transferring models. Whilst spatial transferability studies retain prominence in the literature (and thus in this manuscript), this is not an indication of relative importance, but rather a reflection of the inherent difficulties in evaluating models transferred through time. Our review of published studies is not exhaustive, and the online supplementary information provides additional literature relevant to each challenge.

## Fundamental Challenges

### Is Model Transferability Trait- or Taxon-Specific?

Knowing whether models are more transferable for some taxonomic groups would be useful to increase confidence in predictions and prioritize resources for model development (Box 1).

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Evidence indicates discrepancies in model performance among taxa with divergent life-history traits, and populations with different age structures and sex ratios (e.g., [14]). Meta-analyses demonstrate that body size and trophic position are strong indicators of ecological predictability [15], with some studies also indicating greater hurdles in building transferable models for wide-ranging organisms with broad environmental niches than for narrow-ranging specialists [16]. For example, model transfers for butterflies were less accurate in species with long flight seasons [17]. By contrast, models of vascular plants with higher dispersal ability exhibited better transferability than those built for endemics with limited dispersal capacity [18]. Developing transferable models for species with greater behavioral or adaptive plasticity might also be more difficult, regardless of spatial range size [8]. Subsetting movement and observational data by behavioral state (e.g., foraging versus breeding) or group composition (e.g., presence of mother–young pairs) prior to model calibration might improve model performance and transferability.

### Which Response Variables Make Models More or Less Transferable?

The superior information content inherent to abundance data should facilitate greater transferability than models of occurrence built from presence–absence or presence-only data, so that models of abundance might better project the ecological impacts of global change [19]. While this has been shown for some birds [19], fitting abundance models remains difficult for most taxa [20], not least because counting individuals is more challenging than recording presence–absence (despite issues caused by imperfect detectability). Accordingly, interest has grown in comparing the predictions obtained from occurrence and abundance models, and testing the reliability of the former as a surrogate for the latter [21]. In general, stronger correlations between abundance and occurrence are expected for rare organisms. However, the strength of this relationship can be nonlinear, species-specific, and conditional on spatial behavior, social organization, life-history strategies, population density, resource availability, and **biotic interactions** [22]. Most studies have also applied model transfers to single species. Community- and ecosystem-level models that fit shared environmental responses for multiple species simultaneously could achieve higher transferability [23], but this potential has been inconsistently demonstrated. Integrated models that unite presence-only and presence–absence data [24], and those that combine occupancy probabilities (e.g., derived from regional monitoring) with density-given-occupancy (e.g., derived from telemetry), offer further promise [25]. The former provide more accurate predictions than models based on a single data type, whereas the latter can account for suitable but unoccupied habitats.

### To What Extent Does Data Quality Influence Model Transferability?

More accurate and/or precise data should result in better transfers on theoretical grounds, with evidence showing that the accuracy of species records can be more important for transferability than their spatial extent [26]. Data of unverifiable quality (e.g., anecdotal reports of easily misidentified species) should therefore be avoided, even if available over broader geographical areas. Model transfers can be further hampered by imperfect detectability, spatial and temporal biases in data collection, insufficient sample sizes, the omission of known drivers, or the use of proxy variables [27]. Additionally, species' characteristics such as range size can impact positional accuracy, leading to erroneous predictions if analyses are conducted at scales corresponding with those of the original locational errors [28]. The magnitude of these effects is ultimately unclear, and data quality therefore represents a substantial source of uncertainty [29]. Simulation studies based on virtual species with known reference information represent a critical resource in tackling this knowledge gap.

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### How Can Sampling Be Optimized to Maximize Model Transferability?

Samples encompassing the full range of environmental conditions and their possible combinations should avoid incomplete niche characterization and improve transferability (Box 2). However, data are often collected opportunistically and pooled during analysis, such that model building ought to account for uneven sampling in environmental space (e.g., by including random effects, or through explicit balancing methods that capture the intensity and distribution of sampling effort [30]). Importantly, data resolution influences model fit, prediction, and by extension, transferability. For example, poorly resolved predictors might not capture important aspects of a species' ecology, and relate only indirectly to observed patterns of occurrence and biogeography [31,32]. Where possible, the scale(s) over which the processes of interest operate should therefore drive predictor choice, with sensitivity tests advisable [31]. As habitat availability, and thus perceived preference, also often link to scale [33], models will be sensitive to the extent of the study region, especially for fragmented habitats and steep environmental gradients [8]. As such, combining geographically and environmentally distinct regions ought to increase model transferability [34]. Temporal replication in sampling can also help by capturing natural variability and stochastic processes, as well as alleviating imperfect detectability and false negative rates. When resources are limited, sampling should ideally focus on designs that address existing data limitations and maximize information gain.

### How Does Model Complexity Influence Model Transferability?

Excessively complex models risk overfitting training data and can erroneously attribute patterns to sampling or environmental noise [35], leading to predictions that are biased or too specific to the reference system to be transferable [36]. Greater transferability is thus generally expected in parsimonious models with smooth univariate response curves and few predictors [37]. However, while simple models have been shown to lead to better transferability, they can also yield misleading predictions when transferred to new contexts, implying that simplicity is not always beneficial [38,39]. Ultimately, simple and complex models serve different purposes [40], and in some instances, a preference for accurate and precise predictions over ecological interpretability might be justifiable, making complex models more appropriate [41]. Complex models are also not necessarily more arduous to interpret, and can be valuable for discovering hidden, unexpected patterns [40]. Additionally, they could be useful in exploring nonlinear and dynamic associations of species with indirect predictors across landscapes, seasons, or years [40], to help better accommodate **nonstationarity**. That said, as complexity grows, so do potential predictor combinations and the likelihood of mismatch between reference and target conditions, which can result in incorrect interpolation and **extrapolation** [42]. Species' life-history traits, physiology, or behavior can also influence complexity, such that choosing an optimally complex model requires identifying the most sensible predictors and datasets relative to a given study objective. Novel indices of complexity that emphasize the structural properties of the input data might help [43], as could standardized metrics of predictive performance.

### Are There Spatial and Temporal Limits to Extrapolation in Model Transfers?

While prediction error is expected to increase with 'distance' (e.g., km, days) from reference conditions [1], model transferability appears little related to geographic (and temporal) separation between reference systems and **target systems** (Figure 1). Instead, environmental dissimilarity is what matters most for successful transfers, for which spatio-temporal distances might only occasionally be good surrogates. The minimum level of similarity required to support transferable models, however, remains unknown. Some authors caution against seeking inference beyond one-tenth of the sampled covariate range, yet this rule of

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Trends in Ecology & Evolution

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thumb [44] does not translate into practical and comprehensible guidelines for model end-users (e.g., spatial planners, resource managers). Another solution could lie in the 'forecast horizon', which defines the point beyond which sufficiently useful predictions can no longer be made in any given dimension (e.g., space, time, phylogeny, environment) [45]. Calculating this horizon requires choosing a measure of prediction quality (i.e., a function of accuracy and precision), and a proficiency threshold for 'acceptable' predictions [45]. Both choices can be framed in decision theory and informed through stakeholder participation, making the forecast horizon a flexible and policy-relevant instrument for assessing and communicating ecological predictability.

## Technical Challenges

### How Can Non-analog Conditions Be Accounted for When Transferring Models?

Transferring models into non-analogous environments brings numerous and well-documented perils [46], but the predictive performance of models transferred into novel conditions is rarely tested explicitly [47]. Different techniques to account for **non-analog conditions** will likely be required depending on the degree of environmental dissimilarity (i.e., novel conditions just beyond those observed versus those that are extremely dissimilar). Several tools are available to visualize regions whose characteristics depart from the initial covariate range (e.g., [42,48]), and these can help assess the potential impacts of non-analog conditions on predictive performance. However, these tools cannot predict species' responses to novel conditions, which can be particularly unexpected if environmental change imposes selection pressures that disrupt biotic interactions and cause communities to evolve [49]. Further development of these tools for future transfers, and their application in examining of the outcomes of historical transfers, will improve our understanding on how non-analog conditions can be accounted for when transferring models.

### How Can Nonstationarity and Interactions Be Incorporated in Model Transfers?

Successful transfers rely on the inherent premise that species–environment relationships are stationary at the calibration site and remain so beyond it. However, species' responses to the environment are rarely static, and can vary nonlinearly with resource availability, species ontogeny, and population density [50]. Species–environment relationships are therefore context-specific, and habitat occupation ultimately depends on relative habitat availability [33]. Moreover, anthropogenic activities can strongly influence species' distribution and abundance patterns, and are themselves variable [51]. Disentangling their effects from environmentally driven covariance is difficult, especially when histories of human exposure are unknown, or the magnitude of impacts unobservable. Recent studies have also reconciled transferability with strong evidence for the role of biotic interactions in shaping species' ranges at large spatial scales [52], offering a blueprint for determining when biotic information can support predictions under unobserved conditions. Methods that incorporate functional responses have now progressed to combine data from different regions and use nonstationary model coefficients, enabling enhanced transferability [8,53]. We expect further improvements in knowledge will be made by encouraging the development of models grounded in well-described mechanisms (Box 3).

### Do Specific Modeling Approaches Result in Better Transferability?

Studies have benchmarked the predictive capacity and transferability of existing algorithms under a range of parameterization scenarios, with mixed results (e.g., [54,55]). Random forests and boosted regression trees, two data-driven approaches that are relatively immune to overfitting and can handle predictor interactions, can demonstrate high performance in unsampled areas (e.g., [56]). MaxEnt, another machine learning method, has been ranked

## Glossary

**Anticipatory predictions:** predictions arising from extrapolating the state of a system (ecological or otherwise) either into the future (forecasts), under uncertainty around model parameters (projections), or within systems likely to be impacted by human action (scenarios).

**Biotic interactions:** interactions between organisms, such as predation, competition, facilitation, parasitism, and symbiosis.

**Correlative model:** model fitted to data and relating species occurrence or abundance at known times and locations to sets of environmental (biotic and abiotic) factors. The aim of a correlative model is to describe the conditions proscribing a species' range, thereby generating a quantitative estimate of its geographical distribution.

**Cross-validation:** process of partitioning a dataset into complementary subsets, developing the model on one (i.e., training set) and validating it on the other(s) (i.e., the validation set). Cross-validation is most commonly used to estimate predictive performance; a single final model is often fitted to the full dataset.

**Explanatory predictions:** testable expectations about individual systems, outcomes, or properties, derived from scientific theory. The aim of explanatory predictions is to construct and/or corroborate hypotheses, and establish explanations for the mechanisms underpinning the functioning of natural systems.

**Extrapolation:** process of making predictions to covariate values that are outside the range, correlation structure, or value combinations of those in the training data. Can be spatial, temporal, environmental, or any combinations thereof.

**Fundamental niche:** full set of conditions and resources an organism is capable of exploiting to maintain populations in the absence of biotic interactions, dispersal limitations, habitat degradation, or immigration subsidy.

**Mechanistic model:** model representing causal processes underlying relationships between components of the studied system. Usually developed based on a the most transferable in some studies (e.g., [57]). Generalized linear and additive models have also been identified as robust choices for extrapolation (e.g., [37]), despite potential for generating unrealistic predictions outside the training scope. However, different approaches to model tuning and data treatment contribute to heterogeneity in performance [58], making the suitability of any given technique largely case-specific. A 'silver bullet' algorithm that is best under all circumstances is therefore highly unlikely, and other factors, such as species' characteristics, can sometimes matter more than model choice [59]. Model averaging can avoid overreliance on a single technique by providing a weighted average of competing model predictions [60], and techniques that enable model coefficients to fluctuate in response to changes in habitat and resource availability [53] should improve transferability [8]. In recent years, dynamic models capable of tracking the temporal aspects of a species' behavior and distribution, and joint species distribution models designed to simultaneously account for the co-occurrence of multiple species, have also gained traction. Although still in early stages of development, preliminary findings indicate potential for improved predictive performance [61]. **Mechanistic models** that harness prior biological knowledge within a given system (Box 3) could also enhance transferability, yet remain mostly undertested [62,63].

### How Should Uncertainty Be Quantified, Propagated, and Communicated When Transferring a Model?

Uncertainty arises from many sources [64], including: sampling methodology, species vagrancy, data quality, environmental stochasticity, initial conditions, species identification, model specification, predictor choice, algorithm selection, and parameter estimation [7,45,57]. Improving predictability, and thus decision making (Box 1) [65], requires understanding the origins, propagation pathways, and ramifications of uncertainty, including its spatial and temporal patterns [64]. Model uncertainty is grounded in model assumptions, which underpin the choice of model algorithm, structure, and parameterization [65]. Uncertainty also varies spatially across a species' predicted habitat [66], spreads through the multiple phases of model development (e.g., in hierarchical, multistage models), and has multiplicative effects, such that its magnitude remains generally underappreciated [64]. These are significant challenges, which possibly explain the scarcity of attempts to account jointly for multiple types of variation (but see [29,66]). For this reason, clear protocols for measuring, accounting for, and reporting on uncertainty remain largely lacking. The latter often relates to the model's intended purpose, such that quantifying parameter uncertainty might be a priority when seeking inference about a given predictor, but prediction uncertainty will gain importance when the primary objective is model transfer. Model averaging can help, though it is important to choose a model averaging method that adequately preserves the uncertainty of the combined prediction [64]. Recent advances in hierarchical modeling allow error estimates to propagate through various submodels within one 'integrated statistical pipeline', and could offer a solution in some cases.

### How Can We Best Transfer Models through Time and Evaluate Them in Temporally Dynamic Systems?

All ecological systems exhibit temporal variability, whether predictable (e.g., tides), systematic (e.g., gradual climate warming), or random (e.g., cyclones). Constructing models using the full span (diurnal, seasonal, phenological, and annual) of conditions under which they will likely be applied can address this variation, although distinguishing erroneous predictions from temporally stochastic events in model validations remains a challenge. Time series of environmental variation could help diagnose anomalous conditions falling outside the baseline characteristics of reference and target systems. Studies suggest that some models can project more reliably over centuries [67] than shorter [68] or longer [69] time scales. A fundamental issue for

combination of expert and empirical knowledge of the dominant range-limiting processes that underlie survival and reproduction of the focal species (e.g., physiology, population dynamics, and competitive interactions). In mechanistic models, parameters have a clear biological or ecological interpretation that is defined *a priori*, such that they can be measured independently of the input data. Synonym: process-based model.

**Non-analog conditions:** conditions differing from those currently experienced by a species, including those that do not presently exist. Term often used to describe future climates, but also communities that are compositionally unlike any other found today.

**Nonstationarity:** state of a system in which relationships between variables and by extension, model parameters, do not remain constant through space and time. Antonym: stationarity.

**Predict:** anticipate an unknown quantity or variable before it is observed.

**Realized niche:** portion of the fundamental niche that a species actually occupies, because of constraining effects such as biological interactions or dispersal limitations.

**Reference system:** system in which a model is calibrated before transfer.

**Target system:** system to which a model is transferred.

**Transferability:** capacity of a model to produce accurate and precise predictions for a new set of predictors that differ from those on which the model was trained. For instance, spatially distinct for projections to new areas, or temporally distinct for projections to past or future times. Synonyms: cross-applicability, generalizability, generality, transference.

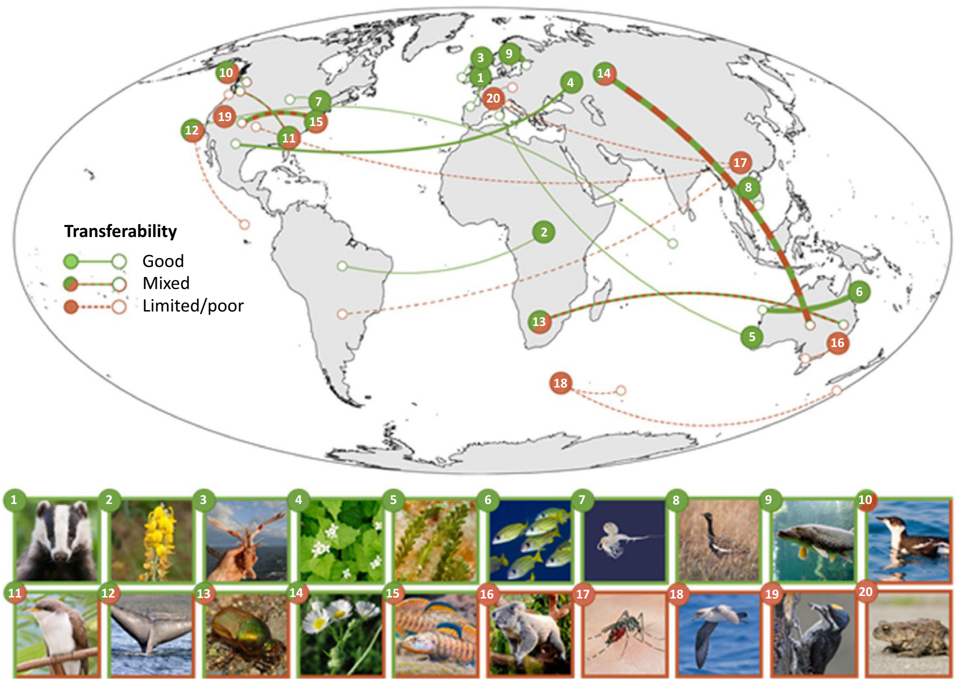


Figure 1. Snapshot of Some Predictive Model Transfers Published in the Ecological Literature. It is commonly assumed that transferability degrades away from the area of calibration. However, geographic separation is often a poor predictor of environmental similarity, such that even models transferred over short distances can yield erroneous predictions if conditions between reference and target sites substantially differ. This paradox is reflected in the contrasting performance of models projected over a range of distances. Here, we showcase studies selected to capture a broad range of taxa (e.g., birds, mammals, plants), ecosystems (terrestrial, freshwater, marine), locations (e.g., Australia, North America, Eurasia), and transfer distances (tens to thousands of km). Colors indicate whether transfers were considered successful (green, unbroken lines; 1–9) or not (dark red, dashed lines; 16–20), as reported by the authors and irrespective of the statistical methods chosen to build the models or the metrics used to evaluate them. Dual colors indicate scenarios in which the quality of transfers varied as a function of modeling algorithms (10–11), space (12), or species (13–15). Line thickness is proportional to the number of modeled species. Reference and target systems are shown as filled and open circles, respectively. Note that, for clarity, not all individual model transfers are portrayed for each study. Photographs depict model organisms and include: (1) Eurasian badger, *Meles meles*; (2) smooth crotalaria, *Crotalaria pallida*; (3) Norwegian lobster, *Nephrops norvegicus*; (4) garlic mustard, *Alliaria petiolata*; (5) invasive seaweed, *Caulerpa cylindracea*; (6) bluestripe snapper, *Lutjanus kasmira*; (7) spiny water flea, *Bythotrephes longimanus*; (8) Bengal florican, *Houbaropsis bengalensis*; (9) northern pike, *Esox lucius;* (10) marbled murrelet, *Brachyramphus marmoratus;* (11) yellow-billed cuckoo, *Coccyzus americanus;* (12) blue whale, *Balaenoptera musculus*; (13) bronze dung beetle, *Onitis alexis*; (14) daisy fleabane, *Erigeron annuus*; (15) rainbow darter, *Etheostoma caeruleum*; (16) koala, *Phascolarctos cinereus*; (17) Asian tiger mosquito, *Aedes albopictus*; (18) grey petrel, *Procellaria cinerea*; (19) black-backed woodpecker, *Picoides arcticus*; and (20) common toad, *Bufo bufo*. References and additional details are given in the supplementary material online.

forecasting is that temporal transfers are often impossible to validate because future events are unknown. One solution is to evaluate predictions of past events (i.e., hindcasting) based on independent historical (e.g., harvest and museum records) or paleoecological datasets, although spatio-temporal, collector's, and taphonomic biases will complicate model calibration and validation [70]. However, for many species of management interest, such records remain unavailable or undermined by issues of spatial or temporal bias, mismatching resolutions between past and present data, and error propagation [71]. Sampling the response variable across its range of habitat variability offers an alternative. This strategy embodies the principle of 'space-for-time substitution', which assumes that spatial heterogeneity across multiple

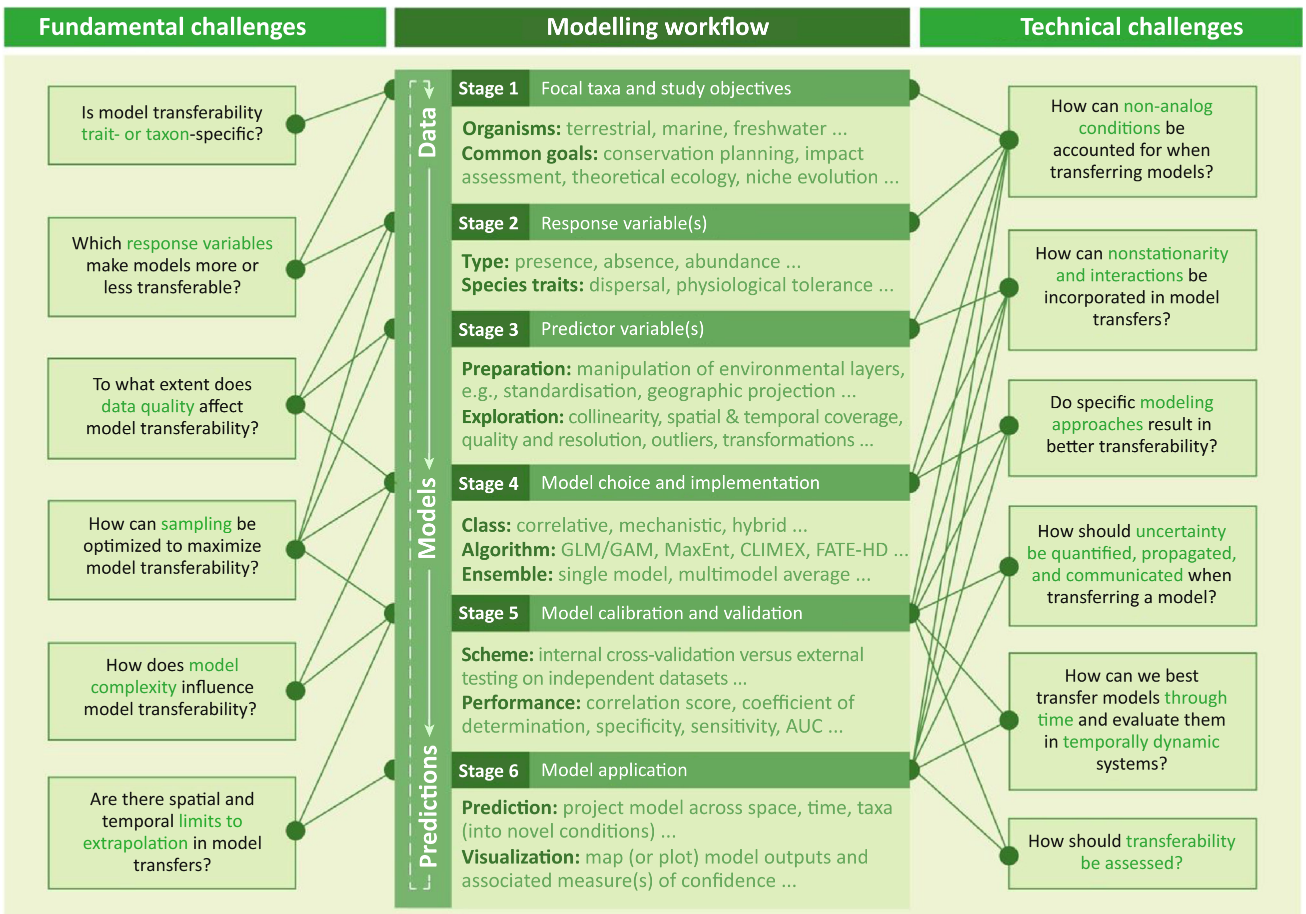


Figure 2. Outstanding Challenges in the Transferability of Ecological Models, and their Relevance to the Modeling Workflow (Adapted from Figure 7 in Robinson *et al.* [12]). Challenges were identified by a consortium of 50 experts. Each directly influences, or is influenced by, one or more stages in the model construction process, from the collection and preparation of data, to the choice of model algorithms and their calibration, validation, and application. Linkages are not intended to be comprehensive, but rather to capture the integral role that transferability plays as an element of ecological modeling practice. Ultimately, fundamental and technical challenges are interrelated in complex ways, such that addressing one may be necessary for, and/or have knock-on effects on, our ability to address any others. The best way to improve our understanding of challenges around model transferability and enhance predictive performance is to use predictions as tools for learning, hence the modeling workflow is a loop representing the ongoing process of learning by doing. AUC, Area under the curve of the receiver operating characteristic; CLIMEX, a mechanistic model of species responses to climate change; FATE-HD, a dynamic landscape vegetation model that simulates interactions between plant species, whilst accounting for external drivers such as disturbance regimes and environmental variations; GAM, generalized additive model; GLM, generalized linear model.

contemporaneous sites at different positions along an environmental gradient can approximate temporal variability [72]. Such would be the case, for example, for areas subject to temperature regimes similar to those anticipated in the future, noting it will not be appropriate for species occupying small ranges or those not well-represented in the fossil record.

## How Should Transferability Be Assessed?

Assessments of transferability demand appropriate diagnostics of prediction accuracy and precision [73], yet there is still little consensus on which metrics are most appropriate [6,74]. All else being equal, true validation is possible only with independent data, which are often

### Box 2. Ecological Niches in Model Transfers

Transferability should be greater in models fitted to observations that document all dimensions of, and constraints placed upon, the **fundamental niche**. However, most datasets fall short of meeting this requirement, because organisms do not always occupy all suitable habitats (or conversely occupy unsuitable ones), either as a result of dispersal barriers, gregarious behavior, anthropogenic disturbances, biotic exclusion (e.g., competition, parasitism), or simply because those habitats do not currently exist [81]. These constraints apply not only to the fundamental niche but also equally to the **realized niche** (i.e., subset of habitats and resources accessible to a given species), meaning that the latter is often restricted in comparison with the former, and that even a perfect understanding of the fundamental niche alone does not make for correct predictions [85]. In practice, failure to fully represent the fundamental niche might lead to truncated response curves that yield unrealistic predictions [38,74], and models that disregard information on absences (e.g., presence-only and environmental envelope models) have been criticized accordingly. While fundamental niches can be expected to stay constant over timescales relevant to management (i.e., daily to decadal), realized niches will typically vary both spatially and temporally. This complicates model transfers, particularly when the realized niche becomes a direct function of habitat selection behavior as it relates to resource availability or physiological tolerance limits [53]. The selection of environmental predictors also impacts the degree to which both fundamental and realized niches can be captured. Emphasis should thus be placed on more direct, functional predictors to foster improved model transfers. Understanding the relationship between niche types can help determine when transfers are more likely to succeed or fail (Box 3), and might be facilitated by jointly modeling target species with their competitors, predators, or facilitators [41]; by coupling distribution and population dynamics models; or by incorporating complex eco-evolutionary factors into model formulations [49] (but likely at the expense of higher data requirements [86]). While mechanistic models (Box 3) are well suited to delimiting species' fundamental niches [87], to date their application remains limited to a few, well-studied taxa for which physiological parameters are documented in detail [4].

### Box 3. Correlative Versus Mechanistic Models

Correlative and mechanistic modeling are two contrasting modeling philosophies that respectively emphasize patterns versus processes [2,87]. **Correlative models** draw statistical linkages between response variables (e.g., species occurrence) and features of the environment (i.e., biotic and abiotic predictors), but have been criticized for failing to explicitly capture the underlying processes (e.g., dispersal ability) that affect said response variable [41]. By contrast, mechanistic or process-based models are built around explicit descriptions of biological mechanisms and parameters that have a clear *a priori* interpretation. If formulated appropriately (e.g., experiment-based parameterizations of species' responses to environmental conditions [62,88]), some mechanistic models can be expected to achieve greater realism, with potential for higher transferability [88]. However, mechanistic models suffer from the same issues of nonstationarity as correlative models, and are thus not immune to potentially inaccurate extrapolation (Box 2). The limited availability of experimental data also remains a major constraint, and it is thus uncertain if mechanistic models can live up to their promise of providing more accurate forecasts of species' range shifts under climate change [62,89]. Indeed, a few studies have found mechanistic and correlative models to perform equally well [63,90]. Mechanistic model implementation also comes at the cost of increased data and computational requirements, limiting their wider use. Although a useful methodological dichotomy, the distinction between correlative and mechanistic models is usually blurred in practice [91] because models within each class rely to some degree on parameterization against observed data, and most ecological mechanisms are actually empirical, rather than theoretical. This need not be detrimental, as it allows a progressive transition from the phenomenological extreme of regression models towards the process-based extreme of mechanistic models. In reality, the approach undertaken will often be dictated by the study context (e.g., availability of prior knowledge). In recent years, arguments have been made for blending correlative and mechanistic approaches, by using mechanistic knowledge as a benchmark for validating correlative models [92], by using mechanistic variables as direct inputs to correlative models [89], or by combining the respective predictions of each model class [93]. Irrespective of the approach chosen, explicitly considering the underlying mechanisms that affect the response is important, and developing a thorough rationale for selecting environmental predictors is crucial to ensure that they are functionally, ecologically, and physiologically meaningful and therefore support transferability [73,94].

unavailable (e.g., a region not yet invaded by a pest) or insufficient (e.g., small sample size). In the absence of validation data for a target site, transferability can only be estimated by contrasting predictions with existing expert knowledge or simulations, and, where feasible, benchmarking performance by projecting models into multiple alternative data-rich scenarios [6]. **Cross-validation** can also provide a reasonable approximation of independence, so long as it can be structured to mimic prediction conditions and minimize correlations (e.g., by deliberately choosing cross-validation folds to emulate extrapolation) [37]. Ultimately, consistent assessments of transferability will require unified and widely applicable standard metrics that enable direct comparisons among studies, systems, and taxa [6]. Instrumental to this are novel approaches to model evaluation and validation (e.g., [75]) that are generally independent of model choice and response variable type.

## Concluding Remarks

Predictions remain a major frontier in ecology [1,45], not least because they are most pressingly needed where we lack sufficient ecological information (Box 1). This leads to a catch-22, where the absence of knowledge encourages the search for transferable models but also impedes their evaluation. Concerted efforts to increase both data quality and data availability are therefore crucial to enhancing the practice of model transfers in ecology [2,76]. Ideally, data should be: unbiased, with explicit coverage of important gradients, high-frequency, long-term, and real-time, so as to maximize opportunities for anticipatory predictions that can be validated with minimal delay [76]. Alternatively, model transfers into novel systems can provide a platform against which data can later be benchmarked once available. Whilst remote sensing, increasingly used in distribution modeling, has the potential to fulfil many of these data ideals, care must be taken to match scales of data to the phenomena that the models are attempting to quantify. Indeed, models that are built with a thorough consideration of ecological processes and the scales at which they operate, even if they are not actually mechanistic models, should have a greater chance of being transferable. Ultimately, the fastest way to enhance predictions is to use them as tools for learning [9] (Figure 2). This necessitates meticulous monitoring of predictive performance, and importantly, rigorous documenting of failures to transfer [20] (Box 4). Quantifying transferability also requires clarity and coherence, yet assessments of model predictions have rarely been harmonized [1]. Without widely applicable transferability metrics that summarize different aspects of predictive success, comparisons between studies will retain little meaning [6]. Indeed, 'How should transferability be assessed?' emerged as the knowledge gap of highest priority during our discussion. Filling this gap appears essential, not only to demonstrate greater levels of transparency in model applications (Box 1), but also

### Outstanding Questions

The question that will arguably always be outstanding is how good is 'good enough'. Inevitably, what constitutes 'satisfactory' predictions from a transferred model will be context-specific, as will be the relative importance of accuracy versus precision. Indeed, developing and transferring models is only the start of the road towards informing decision makers; we also need to ensure findings are accessible and understandable to enable uptake. A great part of this will necessitate effectively quantifying and communicating uncertainty around model predictions. The onus then lies on stakeholders and decision makers to determine what level of uncertainty they are prepared to accept, and at what point uncertain or imprecise predictions from transferred models are better than no predictions at all. As the field of modeling progresses and understanding of transferability improves, we will be able to better inform these discussions, ideally by providing readily comparable transferability metrics and clear measures of associated uncertainties. Ultimately, the question of how good is good enough will always fall to those who use models to make decisions.

### Box 4. Why Can Model Transfers Fail?

Failures to transfer occur for many reasons [95]. Arguably the most obvious is that models tightly fitted to calibration data often do not extrapolate well to novel data [35]. Predictive models also often assume that organisms are at quasi-equilibrium with their environment, such that occupancy or abundance data reflect site suitability. However, biological interactions, disturbance regimes, habitat loss and human impacts (e.g., harvesting), stochastic mortality, or dispersal constraints can prevent species from persisting in or accessing favorable habitats, potentially leading to biased representation of environmental conditions (i.e., a failure to sample the fundamental niche) (Box 2). Species can exhibit immediate responses to one or several components of global change, even though disruptions to networks of biotic interactions can slow down or hasten evolutionary adaptations [96], and population dynamics can lag behind the trend of global change drivers [97]. Nonstationarity can also undermine transferability, because species–habitat relationships vary in complexity, strength, and direction across different ecosystems. The effects of population density on apparent habitat preferences can compromise transferability if increases in population density force individuals into suboptimal areas [50], although modeling the dependencies of habitat coefficients on population density offers a potential solution [8,30]. Numerous datasets additionally suffer from sampling biases as well as spatial and temporal autocorrelation, leading to underestimations of heterogeneity among environmental gradients or populations, which cause problems for fitting and validating models [98]. Where possible, statistical methods for dealing with spatial and temporal correlation should be employed to mitigate these issues [99]. Further bias in predictions can arise from local factors that remain undetected due to the coarse resolution at which most models are calibrated [100]. Mismatched scales between reference and target systems (e.g., temporal range, sampling year, transect size) and the omission of important predictors (e.g., fishing pressure, habitat structure) are among other explanations for models transferring poorly [20,27]. Lastly, failures to transfer can simply ensue from inadvertent stochastic events in the evaluation data, rather than from poor transferability *per se* (i.e., a model might correctly predict the presence of a species, but the validation data do not record the presence due to some stochastic process). Clearly, advancing the application of model transfers in ecology requires increased understanding of the processes and conditions that affect transferability, which will be aided by encouraging researchers to publish the results of unsuccessful model transfers [20].

because transferring models beyond the environments in which they were initially built weakens their credibility and defensibility. Confidence in model predictions will therefore remain limited until we can determine how well models actually perform on independent datasets [64]. Rather counterintuitively, better transferability might not necessarily equate to better decisions if the uncertainties associated with model predictions are not suitably measured, reported, and communicated to end-users and policy makers [13]. So far, a comprehensive treatment of uncertainty and its sources has been too complex and laborious to achieve [2], although significant advances are being made towards this goal. Whilst substantial challenges lie ahead on the road to realizing the full potential of transferable models, the prospective gains are great. As Houlahan *et al.* [1] note, 'transferability is critical to [scientific] understanding because understanding without transferability is [ . . . ] ephemeral and transient'.

## Author Contributions

A.M.M.S., K.L.Y., and P.J.B. conceived the study. K.L.Y., A.M.M.S., P.J.B., M.J.C., and K.M. organized and delivered the conference workshop. All authors formulated challenges and voted on the assembled list. K.L.Y., P.J.B., and A.M.M.S. compiled the data and led the writing of the manuscript. K.L.Y., P.J.B., A.M.M.S., M.J.C., K.M., and C.R. led working subgroups. All authors contributed to the writing of individual sections of the manuscript and provided comments on drafts.

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## Supplemental Information

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## References

1. Houlahan, J.E. *et al.* (2017) The priority of prediction in ecological understanding. *Oikos* 126, 1–7
2. Mouquet, N. *et al.* (2015) Predictive ecology in a changing world. *J. Appl. Ecol.* 52, 1293–1310
3. Verbruggen, H. *et al.* (2013) Improving transferability of introduced species' distribution models: new tools to forecast the spread of a highly invasive seaweed. *PLoS One* 8, e68337
4. Urban, M. *et al.* (2016) Improving the forecast for biodiversity under climate change. *Science* 353, aad8466
5. Clark, J.S. *et al.* (2001) Ecological forecasts: an emerging imperative. *Science* 293, 657–660
6. Sequeira, A. *et al.* (2018) Transferring biodiversity models for conservation: opportunities and challenges. *Methods Ecol. Evol.* 9, 1250–1264
7. Evans, M.R. (2012) Modelling ecological systems in a changing world. *Phil. Trans. R. Soc. B* 367, 181–190
8. Paton, R.S. and Matthiopoulos, J. (2016) Defining the scale of habitat availability for models of habitat selection. *Ecology* 97, 1113–1122
9. Dietze, M.C. (2017) *Ecological Forecasting,* Princeton University Press
10. Werkowska, W. *et al.* (2016) A practical overview of transferability in species distribution modeling. *Environ. Rev.* 25, 127–133
11. Mukherjee, N. *et al.* (2015) The Delphi technique in ecology and biological conservation: applications and guidelines. *Methods Ecol. Evol.* 6, 1097–1109
12. Robinson, N.M. *et al.* (2017) A systematic review of marine-based species distribution models (SDMs) with recommendations for best practice. *Front. Mar. Sci.* 4, art421
13. Pielke, R.A. and Conant, R.T. (2003) Best practices in prediction for decision-making: lessons from the atmospheric and earth sciences. *Ecology* 84, 1351–1358

14. Peñalver-Alcázar, M. *et al.* (2016) Microhabitat selection in the common lizard: implications of biotic interactions, age, sex, local processes, and model transferability among populations. *Ecol. Evol.* 6, 3594–3607
15. Soininen, J. and Luoto, M. (2014) Predictability in species distributions: a global analysis across organisms and ecosystems. *Global Ecol. Biogeogr.* 23, 1264–1274
16. Wogan, G.O. (2016) Life history traits and niche instability impact accuracy and temporal transferability for historically calibrated distribution models of North American birds. *PLoS One* 11, e0151024
17. Eskildsen, A. *et al.* (2013) Testing species distribution models across space and time: high latitude butterflies and recent warming. *Global Ecol. Biogeogr.* 22, 1293–1303
18. Dobrowski, S.Z. *et al.* (2011) Modeling plant ranges over 75 years of climate change in California, USA: temporal transferability and species traits. *Ecol. Monogr.* 81, 241–257
19. Howard, C. *et al.* (2014) Improving species distribution models: the value of data on abundance. *Methods Ecol. Evol.* 5, 506–513
20. Sequeira, A.M.M. *et al.* (2018) Challenges of transferring models of fish abundance between coral reefs. *PeerJ* 6, e4566
21. Weber, M.M. *et al.* (2017) Is there a correlation between abundance and environmental suitability derived from ecological niche modelling? A meta-analysis. *Ecography* 40, 817–828
22. Estrada, A. and Arroyo, B. (2012) Occurrence vs abundance models: differences between species with varying aggregation patterns. *Biol. Conserv.* 152, 37–45
23. Maguire, K.C. *et al.* (2016) Controlled comparison of species- and community-level models across novel climates and communities. *Proc. R. Soc. B* 283, 20152817
24. Fletcher, R.J. *et al.* (2016) Integrated models that unite local and regional data reveal larger-scale environmental relationships and improve predictions of species distributions. *Landsc. Ecol.* 31, 1369–1382
25. Tingley, M.W. *et al.* (2016) An integrated occupancy and space-use model to predict abundance of imperfectly detected, territorial vertebrates. *Methods Ecol. Evol.* 7, 508–517
26. Aubry, K.B. *et al.* (2017) The importance of data quality for generating reliable distribution models for rare, elusive, and cryptic species. *PLoS One* 12, e0179152
27. Sequeira, A.M. *et al.* (2016) Transferability of predictive models of coral reef fish species richness. *J. Appl. Ecol.* 53, 64–72
28. Mitchell, P.J. *et al.* (2017) Sensitivity of fine-scale species distribution models to locational uncertainty in occurrence data across multiple sample sizes. *Methods Ecol. Evol.* 8, 12–21
29. Dormann, C.F. *et al.* (2008) Components of uncertainty in species distribution analysis: a case study of the great grey shrike. *Ecology* 89, 3371–3386
30. Matthiopoulos, J. *et al.* (2015) Establishing the link between habitat-selection and animal population dynamics. *Ecol. Monogr.* 85, 413–436
31. Scales, K.L. *et al.* (2017) Scale of inference: on the sensitivity of habitat models for wide-ranging marine predators to the resolution of environmental data. *Ecography* 40, 210–220
32. Barbosa, A.M. *et al.* (2009) Transferability of environmental favourability models in geographic space: the case of the Iberian desman (*Galemys pyrenaicus*) in Portugal and Spain. *Ecol. Model.* 220, 747–754
33. Beyer, H. *et al.* (2010) Habitat preference: understanding use versus availability designs. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 365, 2245–2254
34. Bamford, A.J. *et al.* (2009) Trade-offs between specificity and regional generality in habitat association models: a case study of two species of African vulture. *J. Appl. Ecol.* 46, 852–860
35. Moreno-Amat, E. *et al.* (2015) Impact of model complexity on cross-temporal transferability in Maxent species distribution models: an assessment using paleobotanical data. *Ecol. Model.* 312, 308–317
36. Bell, D.M. and Schlaepfer, D.R. (2016) On the dangers of model complexity without ecological justification in species distribution modeling. *Ecol. Model.* 330, 50–59
37. Wenger, S.J. and Olden, J.D. (2012) Assessing transferability of ecological models: an underappreciated aspect of statistical validation. *Methods Ecol. Evol.* 3, 260–267
38. Thuiller, W. *et al.* (2004) Effects of restricting environmental range of data to project current and future species distributions. *Ecography* 27, 165–172
39. Evans, M.R. *et al.* (2013) Do simple models lead to generality in ecology? *Trends Ecol. Evol.* 28, 578–583
40. Merow, C. *et al.* (2014) What do we gain from simplicity versus complexity in species distribution models? *Ecography* 37, 1267–1281
41. Zurell, D. *et al.* (2009) Static species distribution models in dynamically changing systems: how good can predictions really be? *Ecography* 32, 733–744
42. Zurell, D. *et al.* (2012) Predicting to new environments: tools for visualizing model behaviour and impacts on mapped distributions. *Divers. Distrib.* 18, 628–634
43. García-Callejas, D. and Araújo, M.B. (2016) The effects of model and data complexity on predictions from species distributions models. *Ecol. Model.* 326, 4–12
44. Dormann, C.F. (2007) Promising the future? Global change projections of species distributions. *Basic Appl. Ecol.* 8, 387–397
45. Petchey, O.L. *et al.* (2015) The ecological forecast horizon, and examples of its uses and determinants. *Ecol. Lett.* 18, 597–611
46. Perrin, E. (1904) On some dangers of extrapolation. *Biometrika* 3, 99–103
47. Torres, L.G. *et al.* (2015) Poor transferability of species distribution models for a pelagic predator, the grey petrel, indicates contrasting habitat preferences across ocean basins. *PLoS One* 10, e0120014
48. Mesgaran, M.B. *et al.* (2014) Here be dragons: a tool for quantifying novelty due to covariate range and correlation change when projecting species distribution models. *Divers. Distrib.* 20, 1147–1159
49. Evans, M.R. *et al.* (2012) Predictive ecology: systems approaches. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 367, 163–169
50. McLoughlin, P.D. *et al.* (2010) Considering ecological dynamics in resource selection functions. *J. Anim. Ecol.* 79, 4–12
51. Street, G.M. *et al.* (2015) Habitat selection following recent disturbance: model transferability with implications for management and conservation of moose (*Alces alces*). *Can. J. Zool.* 93, 813–821
52. Godsoe, W. *et al.* (2015) Information on biotic interactions improves transferability of distribution models. *Am. Nat.* 185, 281–290
53. Matthiopoulos, J. *et al.* (2011) Generalized functional responses for species distributions. *Ecology* 92, 583–589
54. Meynard, C.N. and Quinn, J.F. (2007) Predicting species distributions: a critical comparison of the most common statistical models using artificial species. *J. Biogeogr.* 34, 1455–1469
55. Beaumont, L.J. *et al.* (2016) Which species distribution models are more (or less) likely to project broad-scale, climate-induced shifts in species ranges? *Ecol. Model.* 342, 135–146
56. Mi, C. *et al.* (2017) Why choose Random Forest to predict rare species distribution with few samples in large undersampled areas? Three Asian crane species models provide supporting evidence. *PeerJ* 5, e2849
57. Heikkinen, R.K. *et al.* (2012) Does the interpolation accuracy of species distribution models come at the expense of transferability? *Ecography* 35, 276–288
58. Iturbide, M. *et al.* (2018) Background sampling and transferability of species distribution model ensembles under climate change. *Global Planet. Change* 166, 19–29

59. Guisan, A. *et al.* (2007) What matters for predicting the occurrences of trees: techniques, data, or species' characterictics? *Ecol. Monogr.* 77, 615–630
60. Zhu, G.-P. and Peterson, A.T. (2017) Do consensus models outperform individual models? Transferability evaluations of diverse modeling approaches for an invasive moth. *Biol. Invasions* 19, 2519–2532
61. Zurell, D. *et al.* (2016) Benchmarking novel approaches for modelling species range dynamics. *Global Change Biol.* 22, 2651–2664
62. Kearney, M. and Porter, W. (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol. Lett.* 12, 334–350
63. Kearney, M.R. *et al.* (2010) Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conserv. Lett.* 3, 203–213
64. Beale, C.M. and Lennon, J.J. (2012) Incorporating uncertainty in predictive species distribution modelling. *Phil. Trans. R. Soc. B* 367, 247–258
65. Gregr, E.J. and Chan, K.M. (2014) Leaps of faith: how implicit assumptions compromise the utility of ecosystem models for decision-making. *Bioscience* 65, 43–54
66. Gould, S.F. *et al.* (2014) A tool for simulating and communicating uncertainty when modelling species distributions under future climates. *Ecol. Evol.* 4, 4798–4811
67. Tingley, M.W. *et al.* (2009) Birds track their Grinnellian niche through a century of climate change. *Proc. Natl. Acad. Sci. U. S. A.* 106, 19637–19643
68. Rapacciuolo, G. *et al.* (2012) Climatic associations of British species distributions show good transferability in time but low predictive accuracy for range change. *PLoS One* 7, e40212
69. Varela, S. *et al.* (2009) Is current climatic equilibrium a guarantee for the transferability of distribution model predictions? A case study of the spotted hyena. *J. Biogeogr.* 36, 1645–1655
70. Varela, S. *et al.* (2011) Using species distribution models in paleobiogeography: a matter of data, predictors and concepts. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 310, 451–463
71. Moreno-Amat, E. *et al.* (2017) Incorporating plant fossil data into species distribution models is not straightforward: pitfalls and possible solutions. *Quat. Sci. Rev.* 170, 56–68
72. Anderson, A.S. *et al.* (2013) Current analogues of future climate indicate the likely response of a sensitive montane tropical avifauna to a warming world. *PLoS One* 8, e69393
73. Fourcade, Y. *et al.* (2018) Paintings predict the distribution of species, or the challenge of selecting environmental predictors and evaluation statistics. *Global Ecol. Biogeogr.* 27, 245–256
74. Randin, C.F. *et al.* (2006) Are niche-based species distribution models transferable in space? *J. Biogeogr.* 33, 1689–1703
75. Fieberg, J.R. *et al.* (2017) Used-habitat calibration plots: a new procedure for validating species distribution, resource selection, and step-selection models. *Ecography* 41, 737–752
76. Pennekamp, F. *et al.* (2017) The practice of prediction: what can ecologists learn from applied, ecology-related fields? *Ecol. Complex.* 32, 156–167
77. Addison, P.F.E. *et al.* (2013) Practical solutions for making models indispensable in conservation decision-making. *Divers. Distrib.* 19, 490–502
78. Vanreusel, W. *et al.* (2007) Transferability of species distribution models: a functional habitat approach for two regionally threatened butterflies. *Conserv. Biol.* 21, 201–212
79. Oppel, S. *et al.* (2004) How much suitable habitat is left for the last known population of the pale-headed brush finch? *Condor* 106, 429–434
80. Mannocci, L. *et al.* (2017) Extrapolating cetacean densities to quantitatively assess human impacts on populations in the high seas. *Conserv. Biol.* 31, 601–614
81. Medley, K.A. (2010) Niche shifts during the global invasion of the Asian tiger mosquito, *Aedes albopictus* Skuse (Culicidae), revealed by reciprocal distribution models. *Global Ecol. Biogeogr.* 19, 122–133
82. Tuanmu, M.N. *et al.* (2011) Temporal transferability of wildlife habitat models: implications for habitat monitoring. *J. Biogeogr.* 38, 1510–1523
83. Keller, R.P. *et al.* (2008) Preventing the spread of invasive species: economic benefits of intervention guided by ecological predictions. *Conserv. Biol.* 22, 80–88
84. Doak, D.F. *et al.* (2008) Understanding and predicting ecological dynamics: are major surprises inevitable? *Ecology* 89, 952–961
85. Barve, N. *et al.* (2011) The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecol. Model.* 222, 1810–1819
86. Thuiller, W. *et al.* (2013) A road map for integrating eco-evolutionary processes into biodiversity models. *Ecol. Lett.* 16, 94–105
87. Peterson, A.T. *et al.* (2015) Mechanistic and correlative models of ecological niches. *Eur. J. Ecol.* 1, 28–38
88. Evans, T.G. *et al.* (2015) Mechanistic species distribution modelling as a link between physiology and conservation. *Conserv. Physiol.* 3, cov056
89. Mathewson, P.D. *et al.* (2017) Mechanistic variables can enhance predictive models of endotherm distributions: the American pika under current, past, and future climates. *Global Change Biol.* 23, 1048–1064
90. Robertson, M.P. *et al.* (2003) Comparing models for predicting species' potential distributions: a case study using correlative and mechanistic predictive modelling techniques. *Ecol. Model.* 164, 153–167
91. Dormann, C.F. *et al.* (2012) Correlation and process in species distribution models: bridging a dichotomy. *J. Biogeogr.* 39, 2119–2131
92. Martínez, B. *et al.* (2015) Combining physiological threshold knowledge to species distribution models is key to improving forecasts of the future niche for macroalgae. *Global Change Biol.* 21, 1422–1433
93. Stensgaard, A.-S. *et al.* (2016) Combining process-based and correlative models improves predictions of climate change effects on *Schistosoma mansoni* transmission in eastern Africa. *Geospat. Health* 11, art406
94. Petitpierre, B. *et al.* (2016) Selecting predictors to maximize the transferability of species distribution models: lessons from cross-continental plant invasions. *Global Ecol. Biogeogr.* 26, 275–287
95. Roach, N.S. *et al.* (2017) Poor transferability of a distribution model for a widespread coastal marsh bird in the southeastern United States. *Ecosphere* 8, e01715
96. Van der Putten, W.H. *et al.* (2010) Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 365, 2025–2034
97. Dullinger, S. *et al.* (2012) Extinction debt of high-mountain plants under twenty-first-century climate change. *Nat. Clim. Change* 2, 619–622
98. Araújo, M.B. *et al.* (2005) Validation of species–climate impact models under climate change. *Global Change Biol.* 11, 1504–1513
99. Dormann, C.F. *et al.* (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30, 609–628
100. Randin, C.F. *et al.* (2009) Climate change and plant distribution: local models predict high-elevation persistence. *Global Change Biol.* 15, 1557–1569