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that of the macrobenthos. Meiofaunas also are a crucial trophic connection between microbes and higher levels of production. With their short generations and high microhabitat selectivity, these communities are also starting to be seen as useful ecological indicators.

What do they have to say about

early animal evolution? Seven animal phyla are exclusively meiofaunal, several of which, like the "jewel animal" Loricifera or the Micrognathozoa, were first described only in the last 40 years. Some lineages, like the relatively morphologically simple Acoelomorpha, have been the subject of intense and continuing debate in molecular phylogenetics. A key question concerns whether disparate meiofaunal phyla like gastrotrichs, gnathostomulids, and acoels are small and simple because early bilaterians were also meiofaunal or whether they are secondarily miniaturized from extinct ancestors - a process that clearly does occur, with vivid examples like the hemichordate Meioglossus psammophilus. Recent macrofossil discoveries reminiscent of meiofaunal taxa have begun to change the debate but equally important is the need to hammer down the phylogenetic positions of the extant meiofaunal phyla, which has proven a frustrating challenge.

What are we learning about meiofauna in the 21st century?

With the advent of new techniques from genomics, and of new problems such as widespread microplastic contamination, it's an exciting time for meiobenthologists. Metabarcoding in particular has promise as a tool for rapidly characterizing communities, although database incompleteness and the universality of taxonomically useful primer-pairs remain major issues. Metabarcoding has also cracked open the door on two previously inscrutable areas: meiofaunal microbiomes and diet preferences. The advent of new amplification techniques suitable for long reads also promises to finally enable routine genome assembly from these tiny, heterozygous creatures. New imaging modes such as lightsheet microscopy or nanoscale computed tomography also promise to reveal the adaptations of these

creatures at unprecedented resolution. One happily constant tradition in the meiofauna community is the habit of holding workshops in biodiverse places including taxonomic experts from all meiofaunal groups — a natural approach given the sheer diversity but shared habitat of these creatures, and a sure-fire approach to inspire the next generation with a lifelong fascination for these enigmatic, ubiquitous creatures.

Where can I find out more?

- Balsamo, M., Artois, T., Smith, J.P.S., Todaro, M.A., Guidi, L., Leander, B.S., and Van Steenkiste, N. (2020). The curious and neglected soft-bodied meiofauna: Rouphozoa (Gastrotricha and Platyhelminthes). Hydrobiology 847, 12. https:// doi.org/10.1007/s10750-020-04287-x.
- Cerca, J., Purschke, G., and Struck, T.H. (2018). Marine connectivity dynamics: Clarifying cosmopolitan distributions of marine interstitial invertebrates and the meiofauna paradox. Mar. Biol. *165*, 123. https://doi.org/10.1007/ s00227-018-3383-2.
- Curini-Galletti, M., Artois, T., Delogu, V., Smet, W.H.D., Fontaneto, D., Jondelius, U., Leasi, F., Martínez, A., Meyer-Wachsmuth, I., Niisson, K.S. et al. (2012). Patterns of diversity in softbodied meiofauna: Dispersal ability and body size matter. PLoS One 7, e33801. https://doi. org/10.1371/journal.pone.0033801.
- Gielings, R., Fais, M., Fontaneto, D., Creer, S., Costa, F.O., Renema, W., and Macher, J.-N. (2021). DNA metabarcoding methods for the study of marine benthic meiofauna: A review. Front. Mar. Sci. 8, 730063.
- Giere, O. (2009). Meiobenthology: The Microscopic Motile Fauna of Aquatic Sediments, 2nd edition (Berlin, Heidelberg: Springer).
- Giere, O. ed. (2023). New Horizons in Meiobenthos Research, 1st edition (Cham, Switzerland: Springer Nature).
- Martínez García, A., Bonaglia, S., Di Domenico, M., Fonseca, G., Ingels, J., Jörger, K., Laumer, C., Leasi, F., Zeppilli, D., Baldrighi, E., et.al. (2023). Fundamental questions in meiofauna – how small but ubiquitous animals can help to better understand nature. Preprint at EcoEvoRxiv, https://doi.org/10.32942/X2WP43.
- Mitsi, K., Arroyo, A.S., and Ruiz-Trillo, I. (2019). A global metabarcoding analysis expands molecular diversity of Platyhelminthes and reveals novel early-branching clades. Biol. Lett. 15, 20190182. https://doi.org/10.1098/ rsbl.2019.0182.
- Swedmark, B. (1964). The interstitial fauna of marine sand. Biol. Rev. 39, 1–42. https://doi. org/10.1111/j.1469-185X.1964.tb00948.x.
- Worsaae, K., Sterrer, W., Kaul-Strehlow, S., Hay-Schmidt, A., and Giribet, G. (2012). An anatomical description of a miniaturized acorn worm (Hemichordata, Enteropneusta) with asexual reproduction by paratomy. PLoS One 7, e48529. https://doi.org/10.1371/journal. pone.0048529.

DECLARATION OF INTERESTS

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The Natural History Museum, Cromwell Road, London SW7 5BD, UK. E-mail: christopher.laumer1@nhm.ac.uk

Primer Ecological niche modelling

Wilfried Thuiller

One of the central research questions in ecology and biogeography revolves around understanding the spatial distribution patterns of organisms, the factors influencing species abundance, and why in certain areas there are more species or individuals than in others. Addressing these questions not only forms the bedrock of scientific research in ecology and evolution but also has critical implications for biodiversity conservation and management. To safeguard species, restore habitats, prevent invasions and anticipate future impacts, it is imperative to identify optimal areas for species or biodiversity under current and future conditions, such as changes in climate or land use. Ecologists have long tried to discern which conditions enable species to maintain viable populations in a given area (Figure 1). Broadly speaking, three main conditions must be met for a species to inhabit a site: successful dispersal throughout its biogeographic history; environmental conditions suitable for sustaining a population; and biotic conditions conducive to species persistence, including resource availability and absence of strong competitors. Ecological niche modelling, also known as species distribution modelling or habitat suitability modelling, primarily focuses on environmental factors, though models are increasingly integrating dispersal and biotic interactions. In the following sections, we will delve into the basic structure and hypotheses of ecological niche modelling, their applications and potential future improvements.

A step-by-step approach to niche modelling

Ecological niche models are computational tools that relate observed species occurrence, abundance or biomass data with selected environmental variables. These variables encompass climatic factors, soil conditions, vegetation cover, land use patterns and





Ecological processes



Suitable biotic context (resource, competition) and stochastic processes



Figure 1. Main conditions allowing a species to occupy a given site.

The three main conditions determining a species' occurrence at a site: dispersal limitation, environmental filtering and biotic filters and/or neutral processes, with corresponding geographic space at the successive scales, from global to regional to local (adapted from Guisan *et al.* (2017)).

disturbance regimes — collectively expressing the conditions supporting a species within a multi-dimensional space (Figure 2). The overarching goal is to predict these conditions both spatially and temporally. This process involves several key steps, outlined below.

Data collection

Species occurrence data (locations where a species has been observed) are collected, along with relevant environmental variables, such as temperature, humidity, aspect, soil type and vegetation cover. Species data could either be directly observed in situ or retrieved from georeferenced databases that collect and harmonize global records, such as the Global Biodiversity Information Facility (GBIF) or iNaturalist. The environmental variables can also be measured and quantified in situ (e.g., soil temperature or soil pH from standard protocols) or extracted from georeferenced databases like CHELSA (climate layers at 1 km resolution), SoilGrid (soil information at global scale, 250 m resolution) or Copernicus (repository of remote sensing data at very high resolution, 20 m to 1 km). Note here that as ecological niche models are statistical (correlative), the choice of the environmental variables is essential to avoid spurious or misleading statistical associations. Choice of the sampling design, bias detection, data

cleaning and curation are important parts of this process.

Model training

Subsequently, a model is trained to establish a statistical relationship between the observed occurrences or abundances and the selected environmental variables. The most well-known statistical algorithm for such an endeavor is the general linear model that can accommodate various data inputs (presenceabsence, counts, percentage of cover). Nowadays, the toolbox of researchers has considerably increased with generalized additive models, regression tree-based models and their extension (boosting regression trees or randomForest) or neural networks. These models can accommodate non-linear relationships between species occurrences and the environment but also interactions between environmental predictors.

Model testing

It is not a good practice to train and test a model on the same data as that can provide overly optimistic evaluation, something called 'over-fitting'. Best practices imply using an independent dataset (different area, different protocol). Yet, as such data are rarely available, the original species–environment dataset is commonly divided into two sets: one for model training and one for model testing. Refined approaches involve spatial or environmental stratifications to perform this data split, to test model predictions under various configurations. This split between training and testing is usually repeated several times to get an overall assessment of model quality. Common evaluation metrics include area under the curve of the receiver operating characteristic curve for presence–absence data or root mean square errors for abundance data.

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Model interpretation

If the models prove to be of good quality, variable importance and response curves are key diagnostic elements. Variable importance allows to extract which variables explain most of the variation in species occurrence or abundances. Some variables might not have any effect while others can be instrumental. This step is usually followed by extracting the response curves of the species along those important variables (Figure 2) to quantify the shape of the relationship. For instance, ecological theory predicts a bell-shaped relationship between species abundance and temperature for most endothermal species. In very stressful environments, a sigmoid or linear relationship might be expected instead.

Model prediction

Once the model is trained, tested and interpreted, it can be used to predict the potential distribution of the species or habitats in other areas where occurrence data may be lacking, or in space when the environmental predictors are known and mapped (e.g., CHELSA climate). The model generates a suitability map that indicates the likelihood of the species being present across the study area, or the spatial variation in abundance (in function of what has been modelled, presenceabsence, abundance or counts). When environmental variables are also available into the future (e.g., IPCC scenarios), notably for climate and land use, models can then be used to forecast where suitable areas might be in the future. The prediction assumes the estimated relationship holds wherever the environmental parameters are known. This assumption is also important when considering projecting into future conditions, because it

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implies that the current response of species to a variable, such as annual mean temperature, will remain the same in the future.

Ensemble modelling

As different data collection, sets of environmental variables, algorithms and climate or land use scenarios can lead to different predictions, a common practice is to build ensemble models and predictions. In other words, different algorithms with different parameters are trained on various subsets of the original data, tested and interpreted, and then used to make an ensemble of predictions in space or in time. Such an approach allows extraction of uncertainty parameters, confidence intervals and consensus predictions (i.e., similar to the climatic diagrams showing plausible future climates).

From species distribution models to biodiversity models

Interestingly, while they are commonly usually termed 'species distribution models', the overall approach of statistically relating biological observations to environmental conditions can be applied more broadly. With a twist in the underlying ecological assumptions, the same strategy could be applied to directly model genes, ecotypes, habitat types, aggregated biodiversity measures, such as species richness or functional diversity, and even ecosystem functions and services.

For instance, when modelling habitat type, it is assumed that a habitat type behaves like a super-organism that has specific environmental requirements or preferences that can be measured, quantified and then mapped spatially. When modelling genes or alleles, here again, the basic assumption is that individuals or populations show local adaptations to environmental conditions that can be observed in the expression of genes that can be further quantified and mapped. In essence, the comprehensive statistical framework remains unchanged, involving relating a vector of observations (species, traits or genes) with a matrix of environmental variables.

With the advent of increased computational capabilities, recent advances have facilitated the



Figure 2. Schematic representation of ecological niche modelling.

It starts from observed presence (and absence) data together with either *in situ* environmental information or an available spatial database. Then, statistical models are built to relate the observations to the environmental information. This implies model calibration, tuning, validation on hold-out data, model checking. If models are robust, they are then used to predict back onto space the potential distribution of the species under current conditions. Models built are also used to predict potential future distributions under different scenarios, like climate or land-use change scenarios.

concurrent modelling of multiple species, habitats or traits. This enables the model to potentially glean insights from other species and capture the residual correlation structure among the modeled species. More precisely, for each species prediction, we can also extract the errors (i.e., how far is the modelled prediction from the truth), commonly called 'prediction residuals'. When modelling multiple species altogether, we can thus extract prediction residuals for all species and analyze their correlation. This can help diagnose whether they are some specific patterns in the errors, whether most species are badly modelled under various environmental conditions, or whether there is some spatial structure in those residuals. Examining these residual correlations presents an opportunity to delve into the costructure among species, revealing potential missing key environmental variables, spatial constraints and biotic relationships.

Applications of ecological niche models

Ecological niche models have demonstrated their versatility for understanding and predicting species or habitat distributions across various dimensions. Following the establishment of statistical relationships

between species occurrence or abundance and pivotal environmental variables, several statistical tools facilitate the estimation of the marginal or conditional importance of these input variables. Variable importance is traditionally obtained from the standardized effect sizes from regression-based models or from variable permutations from machinelearning algorithms. Subsequently, partial response plots depict the species' response to the selected variable. This can help understand how a specific factor like soil pH influences the abundance of species bacteria or fungi, or whether there are some critical thresholds enhancing or prohibiting the survival of a given species (Figure 3). This knowledge might prove to be particularly useful for biodiversity management.

Regarding invasive exotic species, ecological niche modelling is also employed to compare how an invasive species uses the available environmental space in its native range compared to its invasive range. Such a comparison helps understand where invasive species might spread to given their known native environmental niches, but also whether invasive species tend to use a different set of environmental conditions than in their native ranges. Such deviations



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Figure 3. Variable importance and response curves for bacterial communities. Variable importance and response curves of bacterial trophic groups in the French Alps in function of sets of climate, soil, phenology, habitat and hydrological variables. On the left panel, the relative importance for each broad environmental class to explain the change in abundance of the trophic groups. The two right panels show the partial responses of selected bacterial groups to soil carbon–nitrogen ratio and soil pH.

may arise if the environmental niche in the native range was constrained by factors, such as predation or disturbance, that might not exist in the new range. Trained models are also used to predict the potential spread of exotic invasive species or to highlight areas that might soon become invaded.

In a broader context, ecological niche models are often used to predict the geographical distribution of species. This includes mapping the probability of species occurrence or variations in abundance within a specified area. With the capability to generate high-resolution maps depending on input environmental variables (ranging from a few meters to kilometers), these maps play a pivotal role in conservation and restoration efforts. This is particularly crucial for safeguarding rare species or preventing the spread of invasions. Amidst the ongoing global change crisis, ecological niche models are also widely employed to forecast potential species or habitat distributions under future conditions. Climate, land use and pollution scenarios are employed to illustrate how various plausible futures may impact species, habitats and overall biodiversity. These projections are then used to test the relevance of existing protected area networks into the future, to reveal future restoration areas or as input of systematic conservation planning to prioritize future areas.

Future improvements

The future of ecological niche models lies in refining their ecological realism by incorporating factors such as biotic interactions and dispersal mechanisms. It is crucial to acknowledge that the environmental variables used to define a species' ecological niche span both abiotic components, like temperature or pH, and biotic components, such as the presence of resources or the influence of strong competitors. Yet, the inclusion of biotic factors is not yet common practice, largely due to the requisite prior knowledge about the resources or competitors specific to the species under consideration. Addressing this limitation, the growing availability of trophic interaction data, which are sourced from observations. expert knowledge or trait-based inference (e.g., considering two species as interacting if the foraging traits of the predator align with the vulnerability traits of the prey), holds significant promise.

A key aspect involves rigorous error propagation along the trophic chain, enhancing the effectiveness of multi-species modelling. For instance, one approach could involve initially modelling and predicting herbivore species based on climatic and vegetation variables. Subsequently, the modelling of secondary consumers could incorporate climate, vegetation, and the predicted abundances of the herbivores, and so on until the top predators. In this case, it is imperative to integrate prediction errors made at each level into the subsequent modelling stages. In this complex modelling framework, Bayesian computing or bootstrap approaches emerge as crucial tools. These methodologies play a pivotal role in handling uncertainties and refining predictions, ensuring a more robust and accurate representation of ecological patterns and processes.

An additional avenue for improvement lies in addressing dispersal movement, particularly in the context of predicting species range shifts resulting from environmental changes or invasion spread. Early models predominantly entertained two extreme scenarios, no dispersal and full dispersal. The former scrutinized current suitable areas and their potential contraction or expansion, while the latter assumed that the modeled species could migrate to any newly suitable area in the future. The reality, however, lies somewhere in between, prompting a shift towards sophisticated ecological niche models equipped with tools that account for ecological continuities, landscape connectivity and dispersal limitations. Novel advances extend to utilizing ecological niche models to constrain process-based models, concentrating on population demography, dispersal events, and occasionally biotic interactions. These hybrid models are poised to emerge as a focal point in research in the forthcoming

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years, offering a comprehensive and integrative approach to elucidate the intricacies of ecological systems.

Integration of artificial intelligence

The integration of artificial intelligence holds great promise in advancing ecological niche models, particularly in handling large datasets and extracting complex patterns. Broadly speaking, there are two principal avenues through which artificial intelligence, specifically machine learning and deep learning algorithms, can enrich ecological niche models.

The first avenue leverages the prowess of machine learning and deep learning in handling extensive datasets and navigating complex relationships. Models such as Multilayer Perceptron demonstrate the capacity to accommodate a large number of species (e.g., several thousand) within a single model, spanning millions of pixels in a matter of hours - a capability barely fathomed in ecology just a few years ago. This efficacy enhances the utility of burgeoning citizen datasets like eBird, iNaturalist or GBIF, enabling the extension of model applications beyond the traditional focus on vertebrate species to encompass invertebrates.

The second avenue is the use of images instead of tabular information. Historically, researchers related observed samples with vectors of environmental measures (e.g., pH, humidity), either obtained in situ or sourced from extensive databases. In contrast, deep-learning models can proficiently use images from remote sensing. In this paradigm, the model transcends learning from singular pieces of information, instead assimilating insights from a comprehensive spatial and environmental context around a given point. Convolutional neural networks, predominantly employed in face recognition, emerge as the most relevant tool for this application, because they excel in reducing the complex, multilayer information inherent in datasets like multispectral imageries or radar data collected from observed samples. This innovative approach inaugurates a nascent realm of research dedicated to unraveling how landscape structure and complexity can elucidate species and habitat distributions.

Ecological niche modelling or species distribution modelling has evolved into a cornerstone of ecological research, offering valuable insights into the understanding of species-environment relationships. As we move forward, the incorporation of biotic interactions and dispersal dynamics and the integration of artificial intelligence technologies will undoubtedly increase the precision and applicability of ecological niche models, reinforcing their role as key tools for guiding conservation efforts and unraveling the mysteries of the natural world.

DECLARATION OF INTERESTS

The author declares no competing interests.

FURTHER READING

- Chauvier, Y., Thuiller, W., Brun, P., Lavergne, S., Descombes, P., Karger, D.N., Renaud, J., and Zimmermann, N.E. (2021). Influence of climate, soil and land cover on plant species distribution in the European Alps. Ecol. Monogr. 91, e01433.
- Deneu, B., Servajean, M., Bonnet, P., Botella, C., Munoz, F., and Joly, A. (2021). Convolutional neural networks improve species distribution modelling by capturing the spatial structure of the environment. PLoS Comput. Biol. 17, e1008856.
- Deschamps, G., Poggiato, G., Brun, P., Galiez, C., and Thuiller, W. (2023). Predict first-assemble later versus assemble first-predict later: Revisiting the dilemma for functional biogeography. Methods Ecol. Evol. 14, 2680–2696.
- Elith, J., Kearney, M., and Phillips, S. (2010). The art of modelling range-shifting species. Methods Ecol. Evol. 1, 330–342.
- Guisan, A., Thuiller, W., and Zimmermann, N.E. (2017). Habitat Suitability and Distribution Models: With Applications in R (Cambridge: Cambridge University Press).
- Ovaskainen, O., Tikhonov, G., Norberg, A., Blanchet, F.G., Duan, L., Dunson, D., Roslin, T., and Abrego, N. (2017). How to make more out of community data? A conceptual framework and its implementation as models and software. Ecol. Lett. 20, 561–576.
- Petitpierre, B., Kueffer, C., Broennimann, O., Randin, C., Daehler, C., and Guisan, A. (2012). Climatic niche shifts are rare among terrestrial plant invaders. Science 335, 1344–1348.
- Poggiato, G., Munkemuller, T., Bystrova, D., Arbel, J., Clark, J.S., and Thuiller, W. (2021). On the interpretations of joint modeling in community ecology. Trends Ecol. Evol. 36, 391–401.
- Thuiller, W., Lavergne, S., Roquet, C., Boulangeat, I., and Araujo, M.B. (2011). Consequences of climate change on the tree of life in Europe. Nature 470, 531–534.
- Warton, D.I., Blanchet, F.G., O'Hara, R.B., Ovaskainen, O., Taskinen, S., Walker, S.C., and Hui, F.K.C. (2015). So many variables: Joint modeling in community ecology. Trends Ecol. Evol. 30, 766–779.

University Grenoble Alpes, University Savoie Mont Blanc, CNRS, LECA, Laboratoire d'Ecologie Alpine, F-38000 Grenoble, France. E-mail: wilfried.thuiller@univ-grenoble-alpes.fr

Letter

The overlooked role of unisensory precision in multisensory research

Haocheng Zhu¹, Ulrik Beierholm², and Ladan Shams^{3,*}

In a recent study of perceptual processing in professional football players, Quinn et al.1 compared the susceptibility to the sound-induced flash illusion² (SiFI) of goalkeepers, outfield players and a control group to investigate whether goalkeepers have a better multisensory temporal integration. They found that the goalkeepers perceived the illusion less frequently and had a narrower temporal binding window, and suggested that they had an enhanced tendency to segregate the multisensory signals. The authors attributed the decreased degree of perceived illusions solely to the reduction in the prior tendency of audiovisual integration. Here we present an alternative explanation through a Bayesian causal inference model, suggesting that better unisensory precision in goalkeepers can also account for the observed behavioral outcomes.

Several previous studies have demonstrated that the Bayesian causal inference (BCI) model³ can account for multisensory temporal numerosity tasks such as SiFI very well^{4,5}. While Quinn et al.1 suggested that the differences between groups is due to the difference in the prior integration tendency as per the BCI model, no quantitative analysis was performed to test or verify this hypothesis. This interpretation may overlook the role of unisensory precision for the following two reasons. First, BCI is a normative Bayesian model that makes an inference based on the congruency between sensory inputs as well as prior expectation of a common cause⁶, and the perceived sensory congruence would be impacted by noise in each modality (σ_A and σ_{V} , representing the standard deviations of likelihood distributions associated with auditory and visual representations, respectively)3,7,8 . And second, a prior study of auditory-visual

