Scaling down the ecological niche from populations to individuals: an evidence synthesis approach

Dissertation

in Partial Fulfilment of the Requirements for the Degree of

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born on 29th October 1992 in Thessaloniki, Greece

Gutachter

1. ....
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Datum der Verteidigung: ....

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To my parents, my brother and our cat.

Also, to those who left their country in pursuit of a better future.
And didn't find it.

Introduction

General Introduction

In one of the first systematic studies of animals in history, Aristotle (350 B.C.E.) distinguished different groups of organisms based on their physiology, morphology and way of life. He also associated morphological characteristics with not only feeding strategies, but also with the distinct habitats in which animals live. For example, he noticed that none of the fish species with gills is found in land or air, neither feed in land. However, other species, such as hippos, crocodiles, seals and sea turtles, although living in the water, they need to breathe air and breed on land.

e.g. "Τῶν δὲ δεχομένων τὸ ὑγρὸν οὐδὲν οὔτε πεζὸν οὔτε πτηνόν, οὐδὲ τὴν τροφὴν ἐκ τῆς γῆς ποιεῖται, τῶν δὲ πεζῶν καὶ δεχομένων τὸν ἀέρα πολλά. Καὶ τὰ μὲν οὕτως ὥστε μηδὲ ζῆν δύνασθαι χωριζόμενα τῆς τοῦ ὕδατος φύσεως, οἷον αἵ τε καλούμεναι θαλάττιαι χελῶναι καὶ κροκόδειλοι καὶ ἵπποι ποτάμιοι καὶ φῶκαι καὶ τῶν ἐλαττόνων ζῴων οἷον αἵ τ' ἐμύδες καὶ τὸ τῶν βατράχων γένος· ταῦτα γὰρ ἅπαντα μὴ διά τινος ἀναπνεύσαντα χρόνου ἀποπνίγεται. Καὶ τίκτει δὲ καὶ ἐκτρέφει ἐν τῷ ξηρῷ, τὰ δὲ πρὸς τῷ ξηρῷ, διάγει δ' ἐν τῷ ὑγρῷ." (English translation: "There is no animal taking in water that is terrestrial or aerial or that derives its food from the land, whereas of the great number of land animals inhaling air many get their food from the water; moreover some are so peculiarly organized that if they be shut off altogether from the water they cannot possibly live, as for instance, the so-called sea-turtle, the crocodile, the hippopotamus, the seal, and some of the smaller creatures, such as the fresh-water tortoise and the frog: now all these animals choke or drown if they do not from time to time breathe atmospheric air: they breed and rear their young on dry land, or near the land, but they pass their lives in water.")

Species differ at many levels, but in general, each organism occupies a distinct place in the environment. The fennec fox lives in the desert, the aardvark lives in the savannah and the ocelot lives in the rainforest. However, even on the very same spruce tree, someone will find the Cape May warbler at the top of the crown and the Yellow-rumped warbler at the base or lower branches (MacArthur 1958). Why? Because if both species lived at the top of the tree, resources such as food and nesting sites would be scarce. As a result, competition would constrain the size of both warbler populations. If the two species differentiated their resource use to avoid competition, the spruce tree could host more warblers of both species. The coexistence of species has been studied through the prism of ecological niche theory and competitive exclusion principle.

Figure 1. Illustration showing how different warbler species partition the same spruce tree. Clockwise from bottom, a bay-breasted (*Dendroica castanea*), myrtle (*D. coronata*), Cape May (*D. tigrina*), blackburnian (*D. fusca*), and black-throated green (*D. virens*) warblers. Micheal Kaspari commissioned Deborah Kaspari to create this mixed media work for publication in the October 2008 issue of ESA's Bulletin. CC-BY-SA

Niche (originally a French word, defined as a recess on a wall, usually used for decorative purposes) is used as a metaphor in Ecology to describe distinct environments (at any scale). The ecological niche was initially defined at the beginning of the 20th century (Grinnell 1917), as the place where a species lives. Since its advent, many scientists endorsed the concept, while developing different discipline-specific approaches. The ecological niche has been described in terms of habitat, requirements, resources or impact of a species on its environment (Takola and Schielzeth 2022, McInerny and Etienne 2012a). It is thus a diverse term, which has been used to describe many different aspects of a species interaction with its environment.

The conceptual basis of the ecological niche is the competitive exclusion principle (Pocheville 2015). Organisms struggle for survival and compete over the same resources. Two species, in order to coexist, have to differentiate their niches in at least one aspect so that to avoid direct competition. In the warbler example mentioned above, the Cape May and the Yellow-rumped warbler are co-habiting the same spruce tree. They even use the same food source, insects. However, the former feeds at the top of the tree, whereas the latter feeds at the bottom of the tree. Therefore, although they are located in the same environment, they differentiate their feeding locations. Another famous example is Darwin’s finches, which also live in the same place (Galápagos Islands), but they use different food sources. As a conclusion, interspecific competition and the struggle for survival lead to niche partitioning.

The same principles apply at the intra-population level too; individuals of the same populations compete for the same resources. They can thus differentiate their resource use, in order to avoid competition with conspecifics. This type of niche variation has been reviewed by Bolnick et al. (2003), who reached to the conclusion that individual specialization is not insignificant and is more widespread than heretofore thought. More importantly, they defined individual specialization as the residual variation that is not attributable to sex, age or morph differences. In other words, encompasses the cases where an individual has a much narrower niche than the population’s niche (Van Valen 1971).

Although intraspecific niche variation has been recorded by many early studies (Darwin), the idea of individual niche specialization was based on a seminal paper by Roughgarden (1972), which re-surfaced after the 2000s, and which stated that the total population niche width can be partitioned to within- and between-individual components. Between-individual variation refers to inter-individual differences in resource use and can result from the combination of early-life experiences with the social environment (Bergmüller and Taborsky 2010, Laskowski and Bell 2014, Snijders et al. 2014). Within-individual variation refers to the major shifts in physiology and behaviour that individuals undergo throughout ontogeny.

The majority of studies related to individual specialization focuses on diet and feeding habits (Bolnick et al. 2002). This was shown by Bolnick et al. (2003) in an extensive review of empirical data. Only lately was niche individualization discussed on a different basis, such as social interactions (Layman et al. 2015). Notably, when talking about individual niche specialization, we refer to variation that is not attributable to sex, age or morphological differences (Bolnick et al.

2003; Moran et al. 2022; Dall and Griffith 2014). Montiglio et al. (2013) discriminated between behavioural (specialization) and niche specialization and argued that the links between them are still not clear. However, if we accept behaviour to be part of the niche concept, then we can use the overall term ‘individualized niche’.

Behavioural differences refer to the reactions not only towards conspecifics, but also towards an individual’s environment. Consistent individual differences in behaviour have been variously described as animal personality, coping style, behavioural syndrome or temperament (Dall et al. 2004; Réale et al. 2007; Réale et al. 2010b; Carter et al. 2013; Roche et al. 2016; Sánchez-Tójar et al. 2022). In this thesis, I will use the term animal personality, which is defined as the consistent behavioural reactions of individuals across time and among contexts (Réale et al. 2007; Stamps and Groothuis 2010; Kaiser and Müller 2021).

During the last decade, research has shifted its focus to the manifold ecological consequences of animal personality, as individual differences in behaviour impact the way whereby individuals interact with their environment (Carter et al. 2013). This, in turn, has consequences for their fitness (Wolf and Weissing 2012). Behavioural phenotypes can thus correspond to distinct, individual life strategies (Biro and Stamps 2008).

The study of individual differences in behaviour is based on repeated measures. Each individual shall be measured multiple times, because a single observation might involve a high amount of stochasticity and hence hinders any further inference. Repeated measures of the same individual provide the basis for the description of its behavioural phenotype. Since animal personality is characterized by contextual and temporal consistency (Réale et al. 2007), repeated measurements serve as the only robust method for its quantification (Dall and Griffith 2014).

Figure 2 is a heuristic diagram of the ecological sub-disciplines that are involved in the content creation of this thesis. I have also positioned the three manuscripts on the branches that represent their scientific context. Essentially, I tried to surround the individualized niche concept from all possible aspects and delineate its margins.

BOX 1. The aim of the thesis

The aim of this thesis is to bring structure to the concept of individualized niches. As discussed above, niche individual specialization is not a new idea, but it is mostly focused on the morphology and trophic habits of species. This thesis capitalises on findings from niche individual specialization studies and synthesizes them with insights from behavioural ecology. To achieve this, we adopt the overarching concept of individualized niches, which encompasses all the known aspects of niche individual specialization, plus behaviour.

The scope of the thesis lies at the intersection of ecological niche, behavioural ecology and animal personality. The conceptual amalgam of niche specialization and animal personality research has given rise to a new concept -what I hereafter call ‘individualized niche’. This dissertation was conducted under the aegis of the Collaborative Research Centre TRR-212 “A Novel Synthesis of Individualization across Behaviour, Ecology and Evolution: Niche Choice, Niche Conformance and Niche Construction (NC^3)” – hereafter NC^3. The main goal of NC^3 is to redefine the ecological niche concept at the level of individuals and introduce the individualized niche concept. Essentially, it is an attempt to integrate behaviour, ecology and evolution (Krüger et al. 2021).

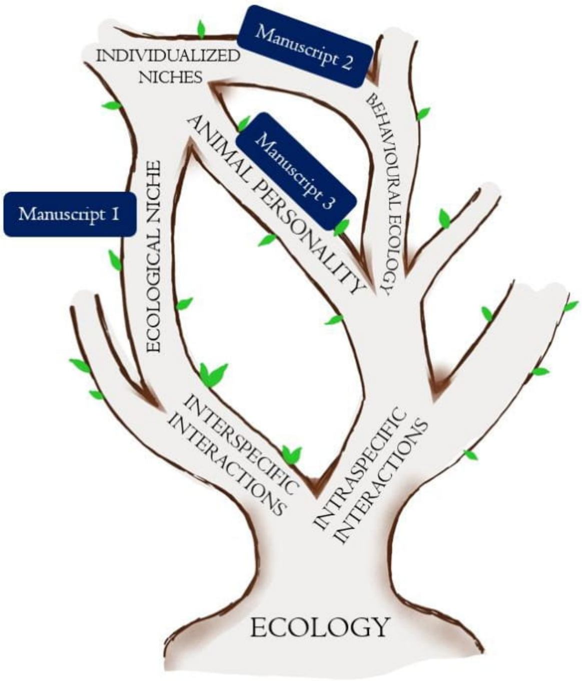

Figure 2. Conceptual context and position of the three manuscripts included in the present thesis.

All projects within NC^3 have studied individualized niches using a smorgasbord of methodologies, ranging from experiments to simulations. However, the scientific discourse among members highlighted the need to define the ecological niche concept in detail, before moving further to the delineation of individualized niche. For this reason, I start with a systematic study of the ecological niche concept (Manuscript 1) and then I proceed with an attempt to (preliminarily) define the individualized niche, while discussing various considerations (Manuscript 2). Lastly, I present a meta-analysis of a behavioural experiment (Manuscript 3), as a case study of individualized niches.

Overview of Manuscript 1

The ecological niche is a core concept in our Collaborative Research Centre NC^3. While discussing with my colleagues, I realized that everyone had a quite particular opinion about what a niche is, depending on their background and expertise. It was thus clear that prior to any discussion about the ecological niche, there is the necessity to agree on a definition.

The ecological niche has been variously defined in terms of habitat, role or requirements of a species. It therefore encompasses a plethora of sub-concepts. The first literature reviews of the concept emerged shortly after its introduction (Hutchinson 1978) and until recently, many studies have attempted to summarize the temporal evolution of the concept (Pocheville 2015; Holt 2009b; Popielarz and Neal 2007; Colwell and Rangel 2009; Koo and Park 2021; Martins 2017). Criticisms of the concept are mainly related to the confusion that this polyphony has casted to ecologists whereas, at the same time, even the usefulness of the concept has been questioned (McInerny and Etienne 2012a). Vagueness and crosstalk have hindered the discourse among ecological sub-fields and more importantly, impeded the communication of scientific results to practitioners.

In Manuscript 1 of my thesis, I explore these sub-concepts using the Research Weaving framework. This framework combines broad-scale and in-depth synthesis while it provides a comprehensive analysis of literature. The aim of this manuscript is to obtain an overview of scientific communities, practices and discourse topics, by implementing the framework on literature relevant to the ecological niche concept. By separating the literature in distinct temporal windows, I was facilitated to identify temporal dynamics and trends of the aforementioned features. The results reflect not only the evolution of scientific conduct, but also the progression of academic culture.

Overview of Manuscript 2

Arguably, one of the most important papers in ecology, is the *Concluding Remarks* (Hutchinson 1957). Although a conference contribution from seven decades ago, this paper is until today very frequently cited. Hutchinson defined the ecological niche concept as an n-dimensional hypervolume in a hypothetical environmental space, where a population has a positive growth rate and can thus persist indefinitely. Any variable that is meaningful to the species' fitness can be considered a dimension of the aforementioned environmental space.

In Manuscript 2, my aim is to explore whether this approach can be applied at the level of individuals. This thought experiment requires the integration of two concepts; ecological niche and animal personality. My starting point is that since individuals differ consistently in their behaviour towards their peers (biotic environment), they should also differentiate their behaviour towards their abiotic environment, resulting in some degree of resource partitioning, with the aim to reduce competition (Bolnick et al. 2007; Schirmer et al. 2020). The concept of individualized niches, as described here, encompasses the ecological consequences of animal personalities as well as all other aspects of intraspecific variation, such as age and sex differences (see also Layman et al. 2015). It therefore includes, but is not limited to, behaviour.

In this review paper, I choose Hutchinson's approach to the niche as the conceptual context of the individualized niche, given that the feature of multi-dimensionality facilitates the downscaling. Any variable significant to an individual's reproductive success can be considered a niche dimension. After introducing a working definition of the individualized niche (in the same vein to Hutchinson's definition), I then proceed to discuss four considerations which arise during this thought experiment.

I can articulate these considerations in the form of four questions:

a) How do we deal with the fact that individuals differ?
b) How individualized niche changes overtime?
c) Which dimensions comprise the individualized niche?
d) Where are the boundaries of individualized niche?

It is not my objective to provide a universal definition for individualized niche, since I believe that this concept can be studied through various prisms. Rather, the aim is to bring structure to the concept and set the scene for further development. It is important to note, however, that if the individualized niche concept is formulated on the basis of a pre-existing niche concept, it will inherit any possible conceptual weaknesses. In any case, some fitness threshold is necessary when defining the individualized niche (Saltz et al. 2016).

Overview of Manuscript 3

In Manuscript 3, I explore individual differences in behaviour from a different perspective: this of animal personality. Animal personality is a major conceptual tenet of the scope of this thesis. The study of animal personality has provided valuable insights regarding intraspecific variation and its ecological and evolutionary significance (Dall et al. 2004). Insights from this field can help us identify the causes of niche individual specialization, because consistent individual differences refer to behaviours not only towards conspecifics, but also towards the environment. Furthermore, the methodological toolbox (O'Dea et al. 2022) used in animal personality can be also used to quantitatively estimate individualized niches, as it includes repeated measures of the same individuals and oftentimes in different contexts (Bell et al. 2009).

The quantitative assessment of animal personalities is achieved through various experimental designs and one popular experiment is the novel object test. In novel object tests, animals encounter an item they have never seen before and their reaction is measured, usually in terms of latency to approach it. Repeated measurements of individuals' reactions result to the assignment of an individual's behavioural phenotype. This experimental design became more prevalent after the 1990s. However, the steps of the process are not fully standardized. On one hand, this gives the freedom to researchers to modify the procedure according to their study species (and research questions), but on the other hand, the use of different testing procedures, makes the results hard to compare across studies.

Our aim here is twofold; firstly, to evaluate whether the novel object test can effectively quantify individual differences in behaviour and secondly, to compare the effect of different testing practices on the observed repeatability of behaviour.

Manuscript 1

Development of the ecological niche concept

Elina Takola, Holger Schielzeth

(In preparation)

Data and code available in:
https://github.com/ETakola/EcologicalNicheEvidenceSynthesis

In 2014, a Curvier's beaked whale (Ziphius cavirostris)
was recorded to dive for 3 hours and 42 minutes
continuously, setting a new world record (Schorr et al. 2014).
Mimicking this individual, we will take a "dive",
in order to find what is hidden in the deep "sea" of literature.
© Elina Takola

FORM 1

Manuscript No. 1

Manuscript title: Development of the ecological niche concept

Authors: Elina Takola, Holger Schielzeth

Bibliographic information: Takola, E. & Schielzeth, H. (2022) Development of the ecological niche concept. *EcoEvoRxiv*.

The candidate is

√ First author, ☐ Co-first author, √ Corresponding author, ☐ Co-author.

Status: in preparation

Authors' contributions (in %) to the given categories of the publication

Author	**Conceptual**	**Data analysis**	**Writing the manuscript**	**Provision of material**
Elina Takola	70%	70%	70%	70%
Holger Schielzeth	30%	30%	30%	30%
Total:	100%	100%	100%	100%

____________________   ______________________________________

Signature candidate   Signature supervisor (member of the Faculty)

“*Ecology’s love-hate relationship with the niche*

has been long and not especially pretty”

(Hairson 1995)

Development of the ecological niche concept

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Data availability statement: Data and code of the analyses in this manuscript are available in https://github.com/ETakola/EcologicalNicheEvidenceSynthesis

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Abstract

The ecological niche is one of the key concepts in ecology. At the same time, there is much debate surrounding its definition and quantitative estimation. In this paper we present a systematic study of over 30,000 studies on the ecological niche. Using an evidence synthesis framework, Research Weaving, we provide an overview of scientific trends over the last 90 years. We explored the study species, the locations of field studies, type of study, as well as scientific patterns of keywords, citations and author collaborations. Furthermore, we used topic modelling to discover hidden semantic topics in the paper abstracts. The most common organisms studied in the ecological niche literature were fungi, bacteria and vertebrates, while the most common study areas were located in China, Brazil, USA and Australia. Some new trends have emerged recently (e.g. the stable isotopes analysis), whereas other trends have fainted (e.g. habitat selection studies). Overall, the ecological niche is clearly and dynamic concept, which encompasses plenty of sub-concepts, as more scientific communities are adopting this term and adjust it to different research contexts.

Keywords: ecological niche, bibliometrics, text mining, evidence synthesis

Introduction

The ecological niche is one of the most influential, but also of the most controversial, concepts in ecology. Although it was first introduced by that name at the beginning of 20th century, the idea of each species' distinct place in the environment dates back to ancient times. Schoener (2009) describes the development of the ecological niche concept as a dialectical process: The inception of the ecological represents the thesis in the first half of the 20th century, lead to the pluralism (antithesis) of the second half (Fig. 1, Schoener 2009). Here we aim to explore whether this dialectical process has moved on to synthesis in recent years, or whether the pluralism remains in literature.

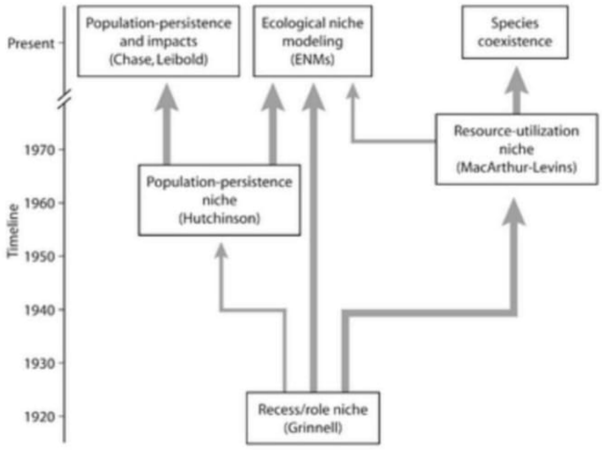

Figure 1. Timeline showing the conceptual development of the ecological niche (Source: Schoener 2009).

The ecological niche was first introduced in scientific discourse by Grinnell (1917), who described the niche of the California Thrasher in terms of habitat and feeding strategies, emphasizing uniqueness of the species. Only a few years later Elton (1927) described niche as the role of the species within its community. Elton's definition emphasizes exchangeability and thus similarity in roles of different species. Even these two very early definitions were thus quite different. Later, Hutchinson (1957), building on previous work by Gause (1934), coined a formal definition of the ecological niche as an n-dimensional hypervolume in a hypothetical environmental space, a definition that still enjoys much popularity. Many more authors followed with similar or different approaches (see Takola and Schielzeth 2022 for an overview). In that vein, the ecological niche has been variously defined as the habitat, the role, the diet of a particular species or its environmental position. This shows that the niche concept is a dynamic and complex notion. Indeed, the first reviews of the concept appeared very early (Hutchinson 1978) and since then many authors provided insights on how niche has evolved (Pocheville 2015; Holt 2009; Koo and Park 2021).

Over the last few decades, the development of complex statistical models and the increase of computational power has given rise to methodologies, which are based in spatial information; i.e. environmental niche modelling (ENM) and species distribution modelling (SDM). Both ENM and SDM now represent large fields of research. In essence, these methodologies treat niche as a multi-factor model, which contains usually abiotic variables (or less often biotic variables) as independent variables and the species presence or the probability of a species presence as a response variable. This approach corresponds to the niche concept as described by Hutchinson (1957). The habitat and climatic conditions constitute an (hypothetical) environmental space and a species actual range (i.e. the occupied areas) is represented by a hypervolume. The goal of ENM and SDM is to map this out in space to arrive at specific predictions per specific species and forecast distributional shifts under environmental change.

A different group of the ecological concept is rooted on the niche concept as described by Elton (1927). Community ecology is the study of the role of a species in terms of its interactions with biotic and abiotic factors. These interactions are measured with the aid of functional traits. Functional traits are characteristics that are directly linked to survival, development, growth and reproduction (Kearney et al. 2021) and are widely used in order to shed light in community dynamics (Wagg et al. 2017; Bartomeus et al. 2016).

Besides the development of different niche definitions, the concept have been applied in practical research. Whether or not the concept have really fueled conceptual development in practice or whether it is mostly of ornamental value is a matter of debate (McInerny and Etienne 2012a). Applications include a diverse array of organisms: plants, animals, fungi, bacteria, algae or cells. In practice, the concept are often modified in order to match the special characteristics of the organism. These kinds of assumptions can potentially be both the cause and the consequence of the plurality of ideas around the niche concept.

While we anticipate that the niche concept will remain pluralistic and will unlikely be unified by a single publication, we deem it useful to review the body of literature that has flourished around the niche concept. Here we explore the ecological niche literature by applying the Research Weaving framework (Nakagawa et al. 2019) on the respective publications. The framework consists of eight components: phylogeny, type/validity, temporal, spatial, contents, terms, authors, citations. We supplement these components with topic modelling to elucidate the morphing of the niche concept as such. We constructed bibliometric networks and systematic maps to provide a conceptual visualization of the ecological niche concept and its development.

Methods

We searched Web of Science and Scopus for keywords relative to the ecological niche concept, using the query “ecolog* AND niche*”. After filtering the results for biology-related categories, we downloaded all publications and their metadata (see Supplement for detailed queries). We included all publications published until and including 2020. The search was finalized on 4th of October 2021 and resulted– after duplicate removal – in 32,833 unique publications.

Phylogenetic distribution of studies

We aimed to assess the diversity of species used in the study the ecological niche concept. For technical reasons, this analysis was based on a random sample comprising 10% of the complete dataset. We extracted the scientific taxonomic names from abstracts and titles using the GNfinder algorithm (Mozzherin et al. 2022). This algorithm searches for specific words in a text, under the assumption that all taxonomic names begin with a capital letter. We then double-checked the results manually and cross-referenced the extracted terms with NCBI (Sayers et al. 2022). Matching with the NCBI database also allowed extracting higher taxonomic units for aggregation.

Type and data source of studies

In order to explore the types of studies within the ecological niche literature, we used the bibliometrix R package to identify document types within our dataset as assigned by WoS and Scopus. However, WoS and Scopus categories are rather coarse. We therefore further classified 50% of our dataset based on the source of their data. We aimed to categorize publications as:

A) Primary data-Observational (original observational data provided with a study);
B) Primary data-Experimental (data from lab experiments or manipulations in the field);
C) Database-based analyses (including paleo-studies, museum specimens/collections and citizen science data);
D) Ideas/concepts/frameworks (no primary data);
E) Methods;
F) Software and applications;
G) Reviews (no primary data);
H) Meta-analysis (results of publications used as data);
I) Simulations.

The classification was done manually using the artificial intelligence platform Rayyan (Ouzzani et al. 2016). Rayyan is an artificial intelligence platform for systematic reviews, where the user can classify abstracts, while training the algorithm.

Temporal trends

To explore the temporal trends of the concept, we used the year of publication and analysed how the number of publications per year changed over time. We combined these trends with the number of search results for the keyword "ecolog*" from Web of Science, to show the relative growth of ecological niche within ecology over the years. We also analyzed temporal trends separately for subsets for such as type or organismal group.

Spatial distribution

The spatial distribution of authors gives us important information about the global patterns of scientific practice. We first extracted the countries from authors' affiliations and aggregated the number of publications by country and year. Then, we visualized the production of each country, as well as the collaboration among countries, using the co-authorship patterns. For the analyses of network changes, which are based on networks and their temporal trends, we calculated three network indices for each subset; degree of centralization, density and diameter. The degree of centralization of a network corresponds to the number of edges per node and thus indicates whether there are nodes of high relevant importance. Density represents the proportion of possible links (edges) that are actually present in the network and thus indicates how well connected are the nodes. Diameter refers to the shortest distance between the two most distant nodes of the network and thus indicates the size of the network. The examination of the trends of these indices allows for a quantitative assessment of changes in network structure.

We also expanded the spatial analysis by identifying geographical information about the location of field studies from titles and abstracts. We used stringr 1.4.0 (Wickham 2019) and maps (Becker et al. 2021) 3.3.0 R packages to identify countries, continents, oceans and seas as well as spacyr and tidygeocoder (Cambon et al. 2021; Benoit and Matsuo 2018) packages to identify location names. We used a list published by Olson et al. (2001) to identify terrestrial ecoregion names. Locations and ecoregions were then aggregated at the level of country and continent (because they might spread over multiple countries, e.g. the European Alps) and visualized as global maps.

Content analysis

We applied a machine-learning algorithm on the abstracts of the publications, with the aim to identify thematic topics within the ecological niche concept. This analysis consists of two stages: pre-processing and topic modelling. Pre-processing is the preparatory stage of the text analysis. It includes removal of frequent terms, numbers, stop words, whitespace and punctuation, as well as word stemming. In the second step, we used the Latent Dirichlet Allocation (LDA) to discover hidden topics in a corpus of texts (Blei et al. 2003; Westgate et al. 2015).

There is no standardized procedure for the evaluation of topic models and we used the following method. Before fitting the LDA model, we used the FindTopicsN() function from the R package ldatuning 1.0.2 (Nikita 2020) to estimate the optimum number of topics in each subset and after fitting the LDA model, we used topic_diagnostics() function from the R package topicdoc 0.1.0 (Friedman 2019) to evaluate the quality of the topics produced.

Finally, in order to facilitate the interpretation of the topic modelling results, we aggregated topics into what we here call “super-topics”, by manually inspecting term overlap.

Trending Terms

With the aim to identify the keywords that were trending over the years, we analyzed keyword frequencies over time, using the fieldByYear() function from the R package bibliometrix 3.1.4 (Aria and Cuccurullo 2017). Keywords can provide important insights in the thematic context of a study, because they are chosen by the authors and essentially represent tags for each publication. Furthermore, keywords often contain information about the method of the study and other secondary information, such as software.

Author influence

Co-authorship patterns represent the culture of science and its change overtime. We constructed networks based on author collaborations using the R package bibliometrix 3.1.4 (Aria and Cuccurullo 2017) and visualized them with igraph R package 1.2.11 (Csardi and Nepusz 2006), to identify communities of authors within the ecological niche literature. Author communities represent lab groups or special research topics. For the analyses of network changes, we followed the same procedure as in Spatial distribution (see above).

To identify clusters of publications sharing the same topic, as well as influential papers within the literature, we constructed historic networks based on co-citations using the histNetwork() function of R package bibliometrix 3.1.4 (Aria and Cuccurullo 2017).

Results

We found 23,895 publications in Web of Science and 24,530 in Scopus. After removing 15,592 duplicates, our final dataset consisted of 32,833 references, published between 1930 and 2022, in 3,298 sources. The increase of the number of publications per year was exponential, though this is likely due to the general development of sciences in the 20th century (see Temporal section). The number of publications before 2000 comprised 8.2% of the dataset and publications after 2010 comprised 66.7%. The information about publication year was not available for 255 references, while 559 abstracts were missing.

Phylogeny

The GNfinder algorithm extracted 7,807 entities. During manual curation of the dataset we identified 5,33% terms that were mistakenly identified as taxonomic names. After removal of the misidentified items, the dataset consisted of 7,390 taxonomic names, from 2,161 publications. In 1,214 publications, there was no taxonomic name identified. The outcome contained many different taxonomic levels (e.g. families, classes, orders, see Table S1), thus we decided to aggregate at the level of Class and Phylum all observations that were identified at lower taxonomic levels (Fig. 2).

The most commonly studied species in ecological niche literature belonged to vertebrates (*Chordata*), followed by invertebrates (*Arthropoda, Mollusca*), plants (*Tracheophyta, Bryophyta*), fungi (Basidiomycota, Ascomycota), bacteria (*Pseudomonadota, Bacillota*) and mosses (*Bryophyta*).

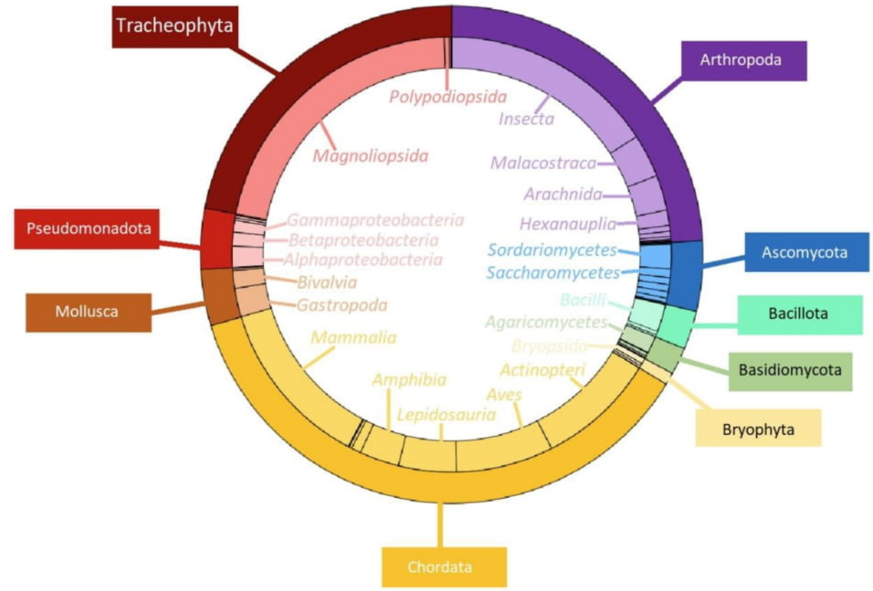

Figure 2. Frequency of the most prevalent Phyla (outer circle) and breakdown to Classes (inner circle) within the ecological niche literature. Phyla with less than 10 publications are not shown

Type of study

The most prevalent document type was journal articles (>85% in all decades, Table S2). We also categorized manually 50% of the publications (n = 16,400 papers) according to the type of study, i.e. based on the source of the data (observations, experiments, simulations, databases etc.). Interestingly, the number of reviews and conceptual papers is not following the trend of the total number of publications related to the ecological niche (Fig. 3). The most prevalent category was “Primary data-Observational” (45.5%), followed by “Primary data-Experimental” (16.9%) and “Database” (15.5%, Table S3), as it is common in ecological niche studies either to collect data in the field or to use databases such as GBIF or citizen science projects, such as iNaturalist and eBird.

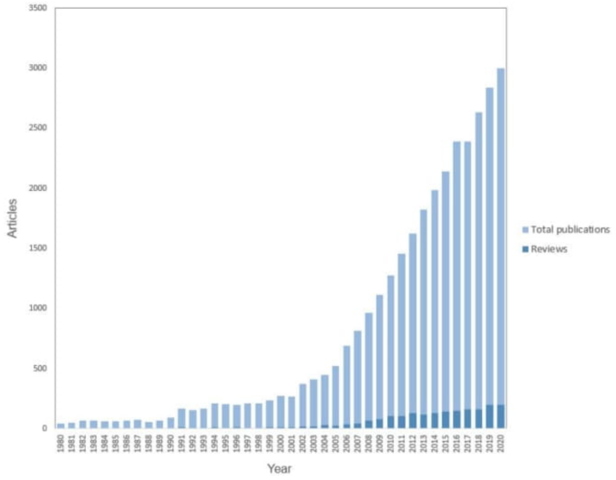

Figure 3. Relevant number of reviews and conceptual papers among the ecological niche literature.

Temporal trends

The temporal trends of ecological niche papers were identified by plotting the number of articles per year. It is important to note here that if we only plot ecological niche articles with year, we observe an exponential growth ($y = 1.3098e^{0.1176x}$). However, this increase is misleading because the absolute numbers of publications have increased exponentially for science in general. For this reason we searched the number of publications for the field of Ecology, by simply searching for the keyword "ecolog*" in Web of Science. In this way, we can present the relative growth of ecological niche within Ecology. The comparison shows that the relative contribution of ecological niche populations within ecology is actually declining.

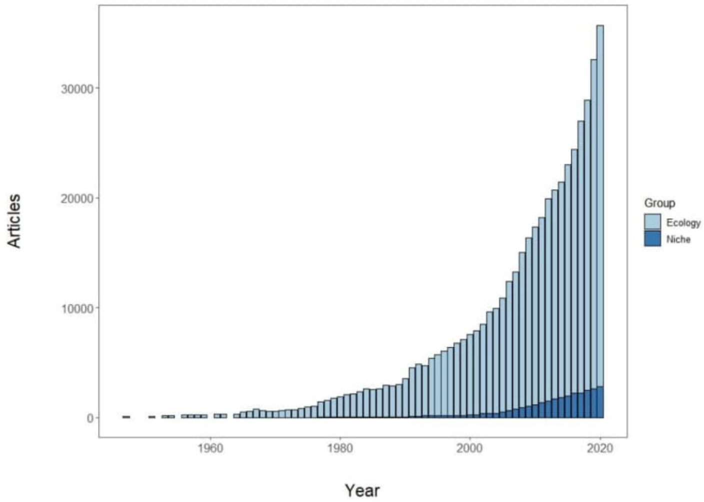

Figure 4. Relevant growth of ecological niche literature within the field of ecology.

Spatial distribution

The analysis of spatial information of the literature had two parts; country networks and extraction of spatial information from abstracts and titles. We constructed country networks to show the global collaboration patterns and we calculated the network indices for each subset. It is clear that ecology has become much more collaborative and multi-country collaborations have significantly increased, but this is a general trend, not specific to the ecological niche (Table S4). We also used text mining to identify location names within abstracts and titles. We also identified countries (Fig. 5), continents, oceas (Table S5) and seas (Table S6).

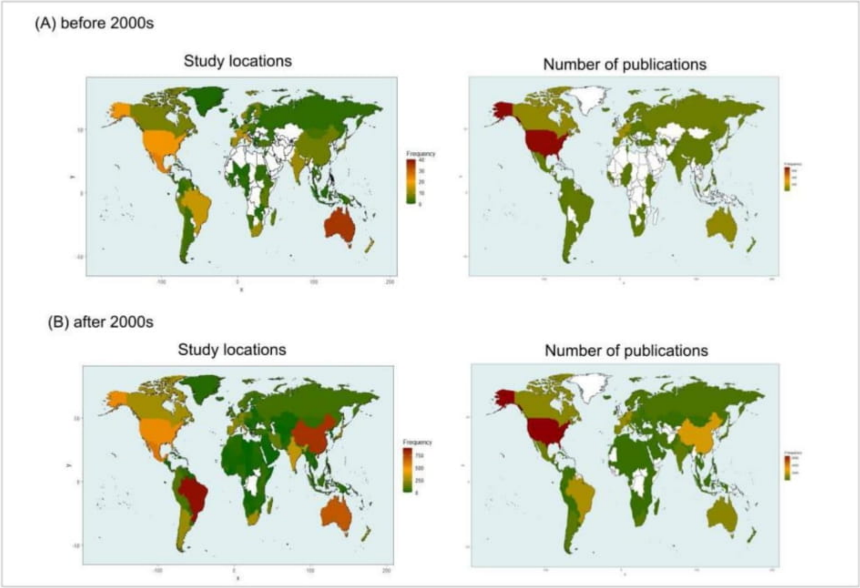

Figure 5. Number of publications (A) before 2000 and (B) after 2000s, based on study locations (left) and author affiliations (right).

Most commonly studied areas were located in Australia, China and Brazil. The most productive country was U.S.A., both before and after 2000s. Interestingly, though, there is a noticeable increase in the number of publications produced by China after 2000. Other places of high ecological importance, appear only as study locations, because they host only a few (e.g. Greenland) or none (e.g. Antarctica) scientific institutions.

Content analysis

We used topic modelling to identify clusters of topics within the corpus of texts on the ecological niche. We repeated the analysis separately for subsets of publications (1930-1990, 1990-2000, 2000-2005, 2005-2010, 2010-2015, 2015-2020). The number of topics for each subset varied from 40 to 110. Each topic comprised of a combination of keywords, grouped together based on their co-occurrence probability. We grouped those topics, based on word similarity, into “hyper-topics” (Table S7). Different topics represent different communities within the ecological niche literature.

Some communities that were clearly identified were plant ecology, ornithology, species distribution models, phylogenetic analyses and aquatic ecology. Some new hyper-topics appeared over time, while other topics declined. For example, urban ecology made its appearance after 2005 and stable isotope analysis after 2000. Chemical ecology disappeared as a distinct topic within the ecological niche literature after 2010.

Trending Terms

We present the keywords frequencies and time range of most prevalent appearance. Climate change and biodiversity are among the most used keywords after 2000s. Keywords, which indicate methodologies to study the ecological niche, are also frequently and increasingly used, for example stable isotope analysis, maxent and ecological niche modelling. On the contrary, other keywords, such as adaptation, character displacement, disturbance, interspecific competition and population dynamics have faded (Fig. 6). This does not mean that these topics are not studied anymore. Rather, they are not popular among ecological niche studies.

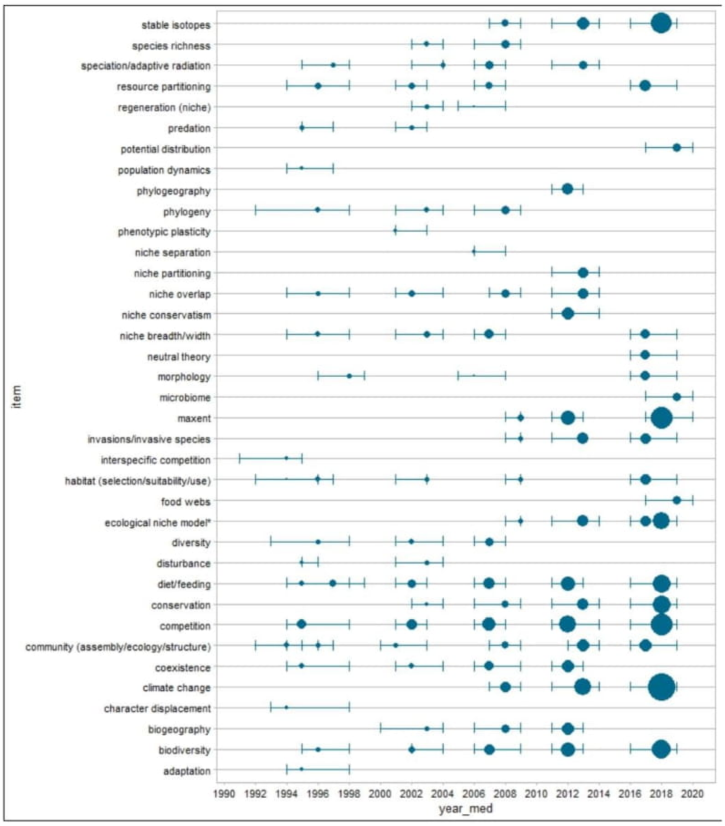

Figure 6. Frequency of keywords for all publications in publications referring to the ecological n (N = 32,833 papers). Size of bubbles represent the frequency of the keywords. The intervals show the years during which each keyword was most prevalent.

Authors

The average number of documents per author dropped from 0.955 to 0.416, because there were only a few single-authored documents, while the average number of co-authors per document increased from 1.1 to 4.81 over the period 1930-2020 (Table S8). Science is increasingly growing and collaboration is nowadays facilitated, also shown by the increase of the diameter and average path length of author networks (Table S9).

Historic co-citation networks

We identified co-citation networks and analyzed how they changed over time. In these network, two papers are connected when they tend to be cited together more frequently than expected by chance. Before 2000s (Fig. A) there are many communities, not very tightly connected and highly dynamic, as they persist for a few years and then they diverge. After 2000s, the network is more dense, bigger and there are more connections between communities. After 2000s, the ecological niche literature is largely dominated by species distribution models (purple) and community ecology (orange). A newly emerged community is shown in light green colour (Fig. 7B) and it is focusing on individual niche specialization.

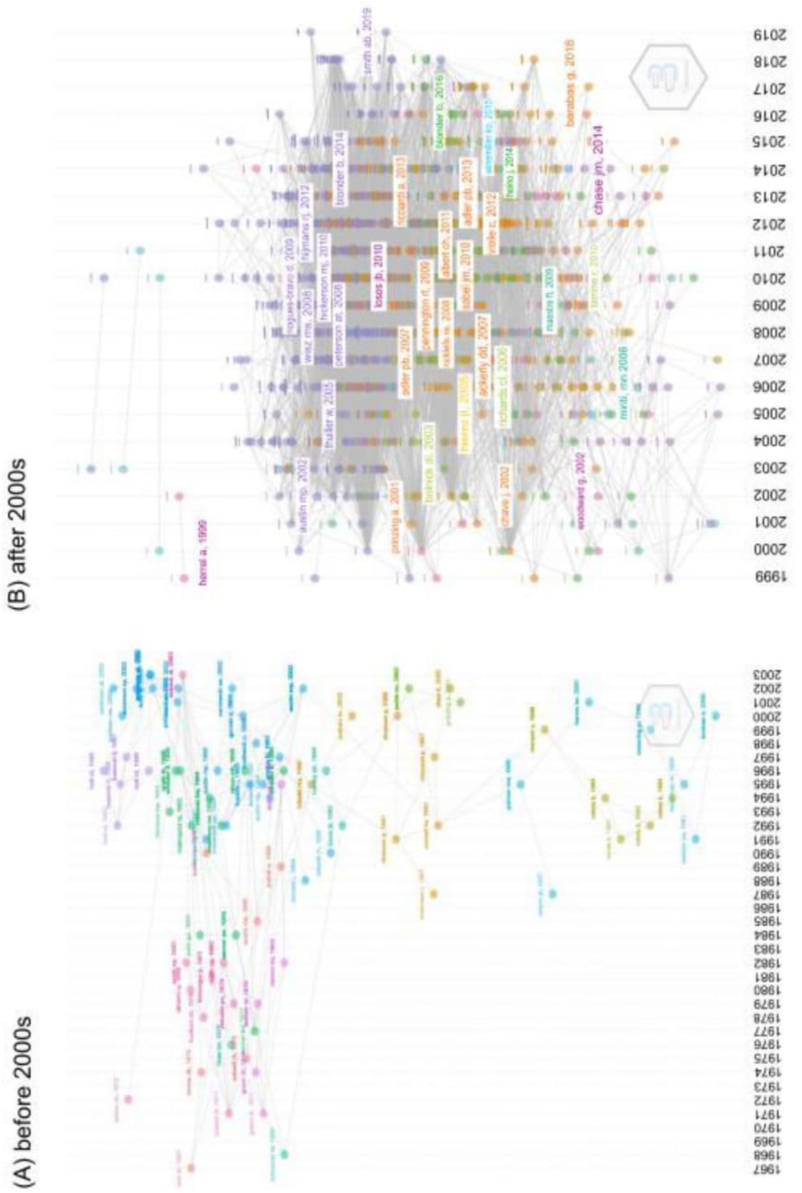

Figure 7. Historic co-citation networks (A) before 2000 and (B) after 2000. Different colours represent clusters of papers that are frequently cited together.

Discussion

We here present an evidence synthesis map of the ecological niche concept. This map shows how the concept has changed over the last 100 years, based on over 30,000 publications. We found that ecological niche literature comprises mainly of studies that include real-world data (either collected in the field, or assembled from a database). The study locations were mostly in USA, Brazil, China and Australia. In addition, a big variety of organisms is used in the ecological niche research; we identified almost 5,000 species, from very diverse taxonomic groups.

The decade 1970-1980 has been an era of plurality for the ecological niche literature, not only due to the increase of new attempts to define the concept (Takola and Schielzeth 2022), but also because more disciplines adopted the concept (Pedruski et al. 2016). According to our topic modelling analysis, after 2000, the literature is dominated by species distribution models, environmental niche models and community ecology. Notably, ecological niche literature has diverged from classic topics to more specific and separable topics, such as urban ecology and the ecology of invasive species.

Despite the fact that the rapid growth of climate change, as a topic, has been observed in many fields of ecology (Westgate et al. 2020; Andrew et al. 2022; Greenville et al. 2017), Craven et al. (2019) found that it biodiversity research has not increased its interdisciplinary character, compared to 1990. Furthermore, the number of papers related to the ecological niche does not follow the increasing trend of ecological papers, suggesting that the term is fading in relative importance. Nevertheless, behavioral ecology of niche specialization represents a comparatively narrow topic, but very distinct, which seems to gain more ground after 2000 and still provides new areas for exploration (Luiz et al. 2019).

Even though we used two sources for our literature search, our dataset was skewed towards journal articles and towards years after 1990. Reviews, both systematic and narrative, are an underrepresented type of publication in ecological literature (Nunez-Mir et al. 2016). Our results were consistent with this observation. Reviews and conceptual papers comprised almost 13% of the papers that we categorized (N = 16,400 papers). Moreover, less than 3% of our dataset comprised of papers published before 1990. The scarcity of publications for the period 1930-1990 is likely because scientists used to publish their research in the form of books, or because niche was not broadly used as a term (McInerny and Etienne 2012b). In addition, many old publications do not contain an abstract (a striking example is Hutchinson's *Concluding Remarks*), causing a temporal bias in our topic modelling results.

Many of the trends observed in our dataset might be just because science and ecology is growing (Réale et al. 2020). For example, the country and author networks have significantly increased in size. Broad collaborations have been found to correlate with higher citation counts (Polyakov et al. 2017). On the contrary, some of the observed results are specific to the ecological niche research. For instance, the diversity of study organisms corresponds with distinct research communities identified by the topic modelling and network analysis. For example, aquatic ecology focuses on algae, clams and fish and macro-ecology on vertebrates and invertebrates.

The analysis of the authorship patterns revealed a caveat. Sometimes, a field study (or sample collection or data gathering from online databases) refers to a specific place, but the author list contains hardly any researchers from this area and as a result, the affiliations of the authors do not represent the places where the study took place. This phenomenon is called helicopter science, parachute research or neo-colonial research (Minasny et al. 2020).

The ecological niche is usually studied through real-world data. The most prevalent study types were according to our classification were primary data and database. Usually, ecological niche studies use the same data sources as biodiversity studies (e.g. IUCN, GBIF). Sampling effort for such databases is not homogeneous across locations, habitats, climatic bioregions, taxa and time (Chase and Knight 2013; Troudet et al. 2017; Meyer et al. 2015; Girardello et al. 2019; Bowler et al. 2022; Geldmann et al. 2016; Beck et al. 2014). Our results confirm this observation, via the uneven distribution of study locations and underrepresentation of certain taxa.

The distribution of study locations is also providing important insights on research practices. Antarctica, for example, shows a strong pattern with fluctuations, which might be the result of funding cycles for expeditions. On the contrary, accessible areas with high ecological importance, such as the Amazon forest and Mediterranean Sea are very prevalent in our database, which was expected – to some degree – as niche and biodiversity research go hand-in-hand (Chase and Myers 2011).

Although many ecologists criticize the ecological niche for being vague and tautological (McInerny and Etienne 2012a; Peters 1976), opinion surveys of ecologists show the importance of the concept for scientific research. In a 2014 survey, members of the Ecological Society of America (ESA) ranked the niche on the 17th place, whereas in 1986 members of the British Ecological Society (BES) on the 7th place regarding its usefulness (Reiners et al. 2017). Hence, what's the future of the ecological niche?

Soberón (2007), in an important review on niches and distributions, suggested an integration of the three most-used approaches of the niche; data on species distributions can be distinguished in environmental variables (Grinnell's approach) and biotic interactions (Elton's approach), while Hutchinson's realized vs fundamental concepts apply to both sets of variables. Alley (1982) suggested a definition that is more evidence-based. We will agree, though, with McInerny and Etienne (2012b) in their claim that we shall adopt an abstract version (holistic term) of the concept when talking at a theoretical (universal) level and decide on its specific features accordingly, whenever we want to apply it in different contexts.

There is a call for an integration of more relevant aspects of species ecology in niche modelling (Higgins et al. 2012) as well as temporal dynamics. Ecological niches can be reconstructed either experimentally, by testing some measure of species performance under different conditions, or statistically, using individual fitness functions or species distribution models (Holt

2009). There are types of SDMs that incorporate behaviour, individual-based data (Panzacchi et al. 2015) and physiological traits (Higgins et al. 2012). Interestingly, from our analysis, we were able to spot a perhaps emerging community; the niche individual specialization (Araújo et al. 2011; Bolnick et al. 2003). We expect that this community will grow in the future, as it provides new insights in the ecological niche concept. It is likely that some of the variation that modelers cannot account for, at the broad scale, can perhaps be explained by behaviour or life-history traits.

Overall, ecological niche is being gradually used by more sub-fields of ecology, since it is a plastic concept, which can be shaped according to the needs of each study. It seems that niche as a role and niche as a multi-dimensional entity are the most prevalent surviving perceptions of the niche. This convergence, from multiple definitions to fewer, provides support to the hypothesis that there is some degree of agreement among scientists, which is probably the result of broad synthesis of previous approaches to the concept.

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Manuscript 2

Hutchinson’s ecological niche for individuals

Elina Takola, Holger Schielzeth

Biology & Philosophy (2022)

Grasshopper species provided lots of inspiration for this paper.
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FORM 1

Manuscript No. 2

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The candidate is

√ First author, ☐ Co-first author, √ Corresponding author, ☐ Co-author.

Status: published

Authors’ contributions (in %) to the given categories of the publication

Author	**Conceptual**	**Writing the manuscript**
Elina Takola	60%	60%
Holger Schielzeth	40%	40%
Total:	100%	100%

______________________ ____

Signature candidate Signature supervisor (member of the Faculty)

“*Much of ecology is confused in its goals,*

uncertain of its strengths and inconsistent in its terminology.”

(Rigler and Peters 1995)

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Hutchinson's ecological niche for individuals

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Abstract

We here develop a concept of an individualized niche in analogy to Hutchison's population-level concept of the ecological niche. We consider the individualized (ecological) niche as the range of environmental conditions under which a particular individual has an expected lifetime reproductive success of ≥1. Our concept has primarily an ecological function, as it refers to the match of an individual phenotype to its contemporary environment (niche fit) while we discuss evolutionary fitness as an evaluative parameter of this fit. We address four specific challenges that occur when scaling the niche down from populations to individuals. In particular, we discuss (1) the consequences of uniqueness of individuals in a population and the corresponding lack of statistical replication, (2) the dynamic nature of individualized niches and how they can be studied either as time-slice niches, as prospective niches or as trajectory-based niches, (3) the dimensionality of the individualized niche, that is greater than the population niche due to the additional dimensions of intra-specific niche space, (4) how the boundaries of individualized niche space can be defined by expected lifetime reproductive success and how expected reproductive success can be inferred by marginalizing fitness functions across phenotypes or environments. We frame our discussion in the context of recent interest in the causes and consequences of individual differences in animal behavior.

Keywords Ecological niche theory · Individual differences · Individualized niche · Intraspecific variation · Phenotype-environment interactions · Developmental plasticity

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Introduction

Individuals differ consistently in their behavior and their relations to the environment. We here aim to explore how individual differences can be integrated into the ecological niche concept in order to yield a utile framework of an individualized niche. Many of the individualized niche features, that we discuss here, have metaphorical value that may help in structuring research (or in modelling studies), but some aspects can also be quantified empirically in natural systems. We first discuss recent progress in the study of consistent individual differences in animal behavior. We next briefly review ecological niche concepts and their different definitions. We then discuss the application of the Hutchinsonian ecological niche concept at the level of individuals. Our arguments are based on the idea that since individuals differ phenotypically, they often also differentiate their positions in the environment, eventually generating individualized niches. We structure our discussion of the individualized niche along four key questions: How can we deal with the fact that individuals are not statistically replicated? How can we incorporate time in the study of individualized niches? Which dimensions constitute individualized niches? Where are the boundaries of individualized niches? These four questions, we think, reflect important considerations, when implementing the concept of the niche at the level of individuals.

We write this essay from the perspective of empirically working behavioral ecologists. We therefore envision populations of individually distinct animals such as vertebrates or arthropods. While we are interested in the causes and consequences of individual differences (including, but not limited to, animal behavior), we do not see a particular individual as the object of study. Instead, we strive to understand how individual differences contribute to population-level processes. It is therefore the state and dynamic of population composition that interest us. We, like many other researchers in the field, use statistical summaries at the level of populations to study individual differences. This perspective relies on the law of large numbers and aims to understand general patterns and processes rather than individual life histories.

Being interested in the consequences of individual niche specialization does not mean that we include long-term or evolutionary consequences in the individualized niche definition that we develop here. Whether a particular phenotype will spread in a population depends on how phenotypic variation is inherited and how particular phenotypes perform in comparison to other phenotypes in the population. We see both aspects, inheritance and relative performance, as very important topics, but not directly relevant to the definition of the individualized niche as such. We think of the individualized niche as the current performance of a particular phenotype in the momentary environment. The concept is thus mainly an ecological and functional concept.

Consistent individual differences

Consistent individual differences have been in the spotlight of behavioral ecology for the last two decades (Sih et al. 2004; Réale et al. 2007). There are now hundreds of studies that report on individual differences in behavior across a large array of species, including vertebrates and invertebrates (Bell et al. 2009). A particular interest has been on behavioral traits that represent general reactions towards the environment, especially when these traits are temporally consistent and correlated across contexts (Kaiser and Müller 2021; Dochtermann and Dingemanse 2013). Individually consistent, context-general traits are often called animal personality traits, temperament traits, coping styles or behavioral syndromes (Kaiser and Müller 2021; Réale et al. 2007). A common research framework, relating to consistent individual differences, is the pace-of-life syndrome, which encompasses behavioral, physiological and life-history components. The pace-of-life syndrome has been linked to personality and survival (Ricklefs and Wikelski 2002; Réale et al. 2010), while it has laid the foundations for the study of implications of behavioral variation (Wolf and Weissing 2012).

From an evolutionary perspective, all individual differences that are heritable can evolve by natural selection. Indeed, individual differences in behavior often have a significant heritable basis (Stirling et al. 2002). It has been shown that animal personality differences can be systematically selected for, thus maintaining inter-individual variation in behavior (Dochtermann et al. 2015; Wolf et al. 2007). Furthermore, intraspecific variation affects interspecific interactions and ultimately species' coevolution (Moran et al. 2021). Consequently, the position of individuals in the environment can both be the cause and the consequence of behavioral differences, owing to the individual *x* environment interaction being bidirectional (Dingemanse and Wolf 2013).

Individual differences in behavior have ecological consequences, because they have an impact on the way in which individuals interact with their environment. For example, phenotypic variation can affect population dynamics through polymorphism in resource use (Dall et al. 2012). Indeed, intraspecific competition might as well be a fundamental cause of individual differences in behavior (Bergmüller and Taborsky 2010). Reduced competition over resources – as a result of specialization at the level of individuals – can increase the carrying capacity of a habitat and promote resilience of populations (Wolf and Weissing 2012). Thus, in analogy to community dynamics, resource partitioning among phenotypes can reduce intraspecific competition and facilitate population growth and persistence (Araújo et al. 2011; Layman et al. 2015). Indeed, an extensive review of empirical evidence on the consequences of intraspecific variation showed that inter-individual diversity increases establishment success, range size, population stability and resilience, while it decreases extinction risk and vulnerability to climate change (Bolnick et al. 2011; Forsman and Wennersten 2016). Intraspecific variation in population-related traits can thus alter population and community dynamics (Bolnick et al. 2011; Araújo et al. 2011). We think that an individualized ecological niche concept can provide a fruitful perspective on individual differences.

The ecological niche

The concept of the ecological niche is fundamental in Ecology. The term was initially vaguely defined and used to describe the ecological position, habitat and requirements of species Packard 1894; Grinnell 1917; Allen 1882, see Gibson-Reinemer

2015). First composed definitions of the ecological niche were presented by Elton (1927) and Grinnell (1928). Elton (1927) defined the ecological niche in terms of the species' function within a community and its relations to other species. This view is focused on the functional role of species and is mostly used in community and functional ecology. Grinnell (1928) proposed the ecological niche as the physical place that species are adapted to. According to this definition, niche is a synonym of habitat or position of species in the environment.

The first reviews on the ecological niche emerged quite early (Hutchinson 1978). Since the introduction of the term, the definition of the ecological niche was a topic for debate. Hurlbert (1981) published a collection of more than 20 quotes defining the ecological niche. We expanded this collection of definition quotes to present, resulting in 36 definitions (Table S1). Some of these definitions are only subtly different. However, ecological niche concepts can be broadly categorized into environment-based concepts and function-based concepts. Environment-based concepts include the ecological niche as the habitat/environment (Grinnell 1917, 1928; Gause 1934; Dice 1952; Odum 1959) or as abstract environmental space (Hutchinson 1957; Root 1967; Macfadyen 1957). Function-based concepts include the functional role of a species (Elton 1927; Clarke 1954) or its trophic position (Elton 1950; Weatherley 1963). Some definitions include a combination of environmental requirements and effects on resource availability (Chase and Leibold 2003).

The most popular and widely cited definition of ecological niche was proposed by Hutchinson (1957, 1978). Hutchinson defined the ecological niche as a hypervolume in an n-dimensional (abstract) environmental space that allows a population to persist indefinitely. He distinguished between fundamental and realized niches, which correspond to an ecological niche before and after accounting for interspecific competition, respectively. While the Hutchinsonian niche concept is primarily defined in terms of place in the environment, it does include some functional aspects, in particular owing to the distinction between the fundamental and the realized niche. Rosado et al. (2016) claim that Hutchinson built on Grinnell's idea, while others (Colwell and Rangel 2009; Swanson et al. 2015) argued that the concept of the hypervolume was introduced by Gause (1934). Independently of Hutchinson's source of inspiration, the *n*-dimensional hyperspace is until today a fundamental concept in ecology and evolution. We therefore explore how this concept can be usefully applied at the level of individuals.

The ecological niche of individuals

The recent interest in the study of individual differences highlights current focus on ecological differences between individuals within populations. Here we address the applicability of Hutchinson's niche concept at the level of individuals. Some early work on ecological niches already included discussions on the importance of individual differences within a population. vanValen (1965), for example, pointed out that individuals differ on how they use available resources and that population niche width is driven by the variation between individuals (Niche Variation Hypothesis). Roughgarden (1972) pioneered the idea to use individual differences in trait expression as proxies for resource use. Traits of individuals are here used as substitutes for the environmental dimensions, which are more difficult to measure. Roughgarden's ideas gave rise to a vibrant field of functional trait analyses (Violle et al. 2007). In the meantime, large databases of functional traits have been compiled, in particular for plants (Fraser 2020; Kattge et al. 2020), albeit only part of these data focus on individual differences.

Although the study of intraspecific variation has been neglected for some decades, it revived around the turn of the last century (Bolnick et al. 2003). Individual niche specialization has been studied empirically mostly with a focus on diet, while studies focusing on habitat selection, behavior, or labor division are less numerous (Ingram et al. 2018; Dall et al. 2012; Bolnick et al. 2003). Notably, individualized niches have been even more vaguely defined than concepts of the ecological niche as such Bergmüller and Taborsky 2010; Müller et al. 2020; but see Trappes et al. 2021). This is partly because the concept is broad and encompasses aspects that can better be kept apart. The aim of our essay is to bring structure into the individualized niche concept and provide definitions not only for the individualized niche in the broad sense, but also for facets that are best treated under different (sub-) labels. In our view, there are four main challenges when applying the concept of the ecological niche to individuals: (1) the question of uniqueness, (2) the questions of time, (3) the question of dimensions and (4) the question of boundaries. We first start with a working definition of the ecological niche of individuals before addressing these specific challenges.

Working definition of the individualized niche

Hutchinson (1957) defined the (fundamental) ecological niche of a population as the range of environmental conditions in which a population can persist indefinitely. Indefinite persistence implies non-negative population growth rate in the long term. Scaling down to individuals, we propose a working definition of the individualized (ecological) niche as the range of environmental conditions that provides an expected lifetime reproductive success of ≥ 1 surviving offspring to particular individuals. In outcrossing organisms each offspring has two parents and should therefore be counted only as 0.5 for each parent.

Before going into more detailed aspects of our individualized niche concept, we want to highlight two important points: First, lifetime reproductive success (commonly used as a measure of absolute fitness) serves as the currency of the phenotype-environment match in our concept and not as the determinant of contemporary selection. This aligns with the Hutchinsonian niche being an ecological, rather than evolutionary, concept. Research on how the individualized niches evolve might have to consider the comparative performance (relative fitness) of alternative phenotypes, including an adjustment for the mode of reproduction. Second, we highlight that the individualized niche, as used in this manuscript, is defined by the environment that an individual lives in, not by its phenotype. The phenotype can act as a mediator that affects fit to the environment (Trappes et al. 2021), but does not represent a part of the niche itself.

The question of individual uniqueness

One issue when defining niches at the level of individuals is that individuals are (by definition) not identical, impeding statistical replication. The ecological (Hutchinsonian) niche of a population can be estimated by quantifying the (hypothetical) areas where different members of a population can be found in the environmental space. Here, individuals serve as replicates at the level of the population and can thus occupy the same niche. However, individuals themselves can only be found at a particular point of environmental space. (We leave the discussion of integration over time for the following section.) Hypervolumes at the level of populations become points in environmental space at the level of individuals. In loose analogy to Hutchinson's realized niche, we call each of these points the *realized individualized niche*. However, the point where an individual happens to live almost certainly does not cover the range of environmental conditions under which it could have occurred. The *potential individualized niche* thus includes all environments where a particular individual would (or could) have an expected lifetime reproductive success of ≥1 (Fig. 1). This means that the potential individualized niche is defined by a space of unobservable outcomes. How can we deal with the problem that realized individual-

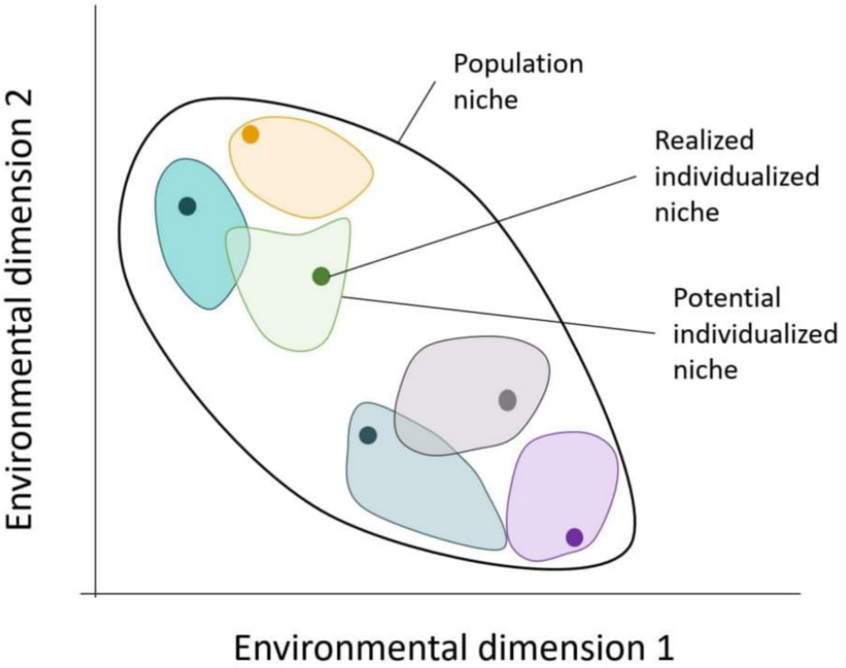

Fig. 1 Schematic view of how realized and potential individual niches occupy subspaces of the population niche. Realized niches are points (or small volumes) in environmental space that occupy only part of the volume that could potentially be occupied by an individual

ized niches are incidental instantiations of points in environmental space and that potential individualized niches are unobservable outcomes?

There are at least partial solutions to both issues. A common approach in the study of realized individualized niches is to address the question on the level of populations and to integrate over time. If we collect repeated observations per individual over short but meaningful time intervals, we can use variance decomposition approaches to quantify population-level variability in realized niches. One approach is the estimation of individual-level repeatabilities that quantify the proportion of variation that is explained by individual differences (Nakagawa and Schielzeth 2010; Bell et al. 2009). The idea here is to treat individuals as ephemeral instantiations, but to view the population-level individual variation as a stable population-level feature of the magnitude of individual differences in realized individualized niches.

Even with replicates over short meaningful time intervals, it is *de facto* impossible to cover the full potential niche of an individual. At least in observational studies under natural conditions, environmental covariation in space and time will prevent individuals to be observed across the full range of potential environments in which it could have an expected lifetime reproductive success of ≥ 1. Experimental approaches offer a partial solution if individuals can be translocated to a range of different environments (Wilson et al. 2019). Some measure of current performance can then be used as a proxy of reproductive success across a range of environments (sacrificing the value of a fixed boundary for defining the niches, see discussion below). However, experimental approaches are necessarily limited to a few dimensions of environmental space. An ultimate limit to experimental exploration of the potential individualized niche is also set by the lifespan of an individual, since potential individualized niches are almost certainly substantially larger than realized niches.

An alternative approach is to marginalize across phenotypes (or genotypes) when mapping individualized niches (Fig. 2). This is rooted in Roughgarden's (1972) idea to use traits of individuals as proxies for resource use. Individuals are here used as replicates to establish a distribution of phenotype-specific environments. In principle,

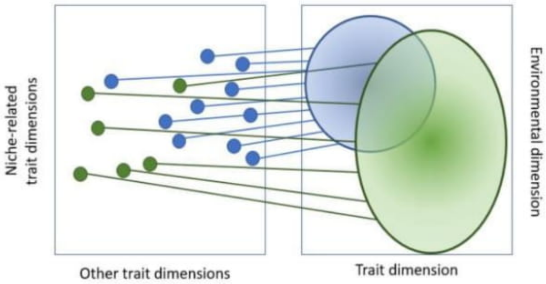

Fig. 2 Schematic view of the idea of using population-level patterns to predict individualized niches and fitness consequences. Colors show different types of individuals (e.g. females and males). The left plot shows two trait dimensions of which one is informative for occupancy of specific environments. The right plot shows a multivariate fitness distribution that depends on phenotype (here shown by different colors on the abscissa) and environments. Fitness arises from the combination of phenotypes and environments. Darker colors show higher fitness expectations

this can be done across many different traits. While individuals are used as tokens of types in particular phenotypic dimensions, individuals are typically unique in their trait combinations. In principle, it would be possible to predict an individual's niche from its unique combination of traits. Such predictions are also possible for non-linear relationships, provided that the form of the mapping function is known. A limit is set only if interactions between traits are strong and poorly replicated in a population. In such cases, trait combinations in some individuals might be so unique that prediction becomes impossible, a limit that is shared with phenotypic novelties.

Both realized and potential niches might be of interest to ecologists. In some cases, the environmental space that is occupied by an individual might be incidental. In other cases, however, features of an organism might influence the realized niche space that can be occupied. Many insect species, for example, show developmentally plastic wing length polymorphisms (Harrison 1980; Zera and Denno 1997). Wing length affects dispersal abilities and thus the range of environments an individual can reach. Short-winged individuals might, in principle, be able to survive and reproduce in very diverse environments (thus they might have a wide potential niche), but in reality, they are limited to the realized niche at their local patch. The developmental pathway to develop long-winged, dispersive phenotypes might not affect the potential niche as defined above, but might result in a much wider array of realized individual niches. Sampling of environments is only possible for an individual with sufficient mobility.

We may distinguish a third form of the individualized niche, the *fundamental individualized niche*. The difference to the potential individualized niche is very subtle and probably not too relevant in practical applications, so the two might often be used interchangeably (see Trappes et al. 2021). Huntchinson's fundamental ecological niche is the environmental space that is occupied by a population in the absence of specific environmental factors (competitors, predictors, dispersal barriers). This is appropriate for populations, because if a species is absent from a potentially suitable habitat, it is so for a reason. Individuals, however, exist only as a single copy and can be absent from many suitable environments, not for specific, but for arbitrary or random reasons (e.g. being born in a specific place). The term fundamental individualized niche might thus be used when there is an absence of particular external (usually intraspecific or interspecific) factors, while the term potential niche does imply coincidental absence from some environments – simply because individuals cannot be at multiple places at a time. The reference space of the potential individualized niche is usually the realized niche of the population, while the reference space for the fundamental environmental niche are all possible environments. The distinction is specific to the individualized niche, since replication is less of an issue for the niche of the population.

Definition A: The *realized individualized niche* is the place in environmental space in which a particular individual is found and has an expected lifetime reproductive success of ≥ 1. The realized individualized niche can be quantified empirically.

Definition B: The *potential individualized niche* is the volume in environmental space in which a particular individual could be found with an expected lifetime reproductive success of ≥ 1. The potential individualized niche cannot directly be quantified, but significant parts of the niche space can usually be statistically inferred.

The question of time

We have alluded to the integration across intervals of time above. This raises the more general question about whether the individualized niche refers to slices of time or to entire lifespans. The ecological niche of a population is focused on entire lifespans. The ecological niche of a forest-dwelling frog, for example, includes a network of forests and ponds, since adults require shelter in woodlands while in its juvenile stage, as a tadpole, the frog requires ponds for survival and growth. Population persistence can only be achieved if both habitats are available. One might argue that the equivalent is also true for individuals: that the individualized niche is a lifetime niche. However, there are arguments why this simple application of lifetime niches misses important intricacies of the individualized niche.

Throughout an individual's life, developmental decisions influence the niche space later in life (West-Eberhard 2003). The development of long wings in grasshoppers, for example, is triggered by increased population density (Poniatowski and Fartmann 2009). All (or at least most) individuals seem to have the potential to develop the long-wing phenotype under high population density, but remain short-winged under low population density. Potential niches of long- and short-winged individuals are therefore no different at birth, since all (or at least most) individuals have the potential to develop into either phenotype. It is a specific time during development when niches of short- and long-winged phenotypes split. Another example is given by match-based phenotypic adjustments. Some species of grasshoppers, for example, are able to change their body coloration during development (Rowell 1972; Dearn 1990). Since body color affects background-dependent crypsis, individuals of different color morphs have different individualized niches in the sense of environmental conditions under which they can survive and reproduce. At birth, these individuals have the same potential for alternative body colors, therefore they have the same potential individualized niches. However, after phenotypic adjustment, their niches become different. A focus on lifetime niches misses the importance of such critical developmental decisions.

We therefore think that the individualized niche (whether realized or potential) is most fruitfully viewed from two perspectives. A time-slice perspective looks for individual niches within certain life stages or other relevant periods of time (such as different seasons). The study of such *time-slice individualized niches* (Fig. 3) allows insights into individual differences in the use of niche space and short-term phenotypic adjustments. A now-and-in-the-future perspective looks at individual niches with a focus on sensitive phases or developmental switch-points and their lifelong consequences (Sachser et al. 2020). We define this ("now-and-in-the-future") perspective, the *prospective individualized niche* (Fig. 4), as the space of environments in which an individual can survive and reproduce given its current phenotype and

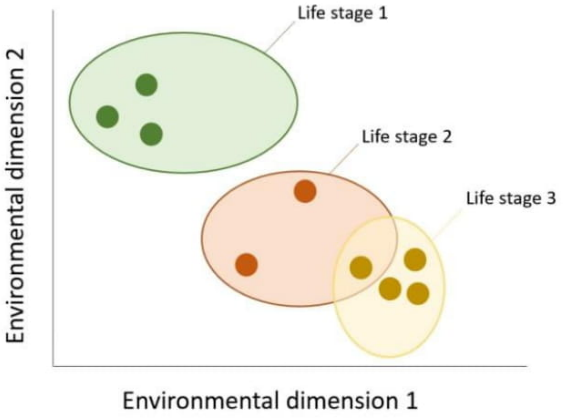

Fig. 3 Schematic view of time-slice niches. Different colors refer to different meaningful life stages of individuals. Filled dots show realized individual niches, while shaded areas show the potential individualized niches

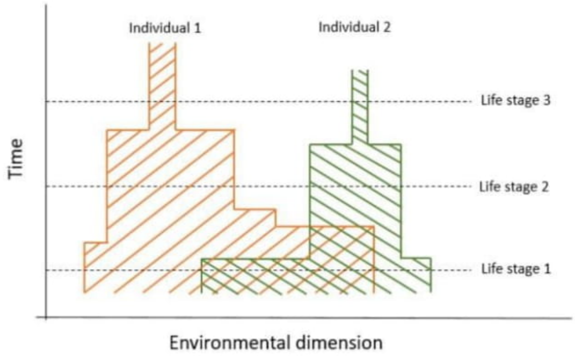

Fig. 4 Schematic view of prospective individualized niches of two individuals. Shaded areas show the potential niche, dashed horizontal lines mark snapshots at three life stages. Steps (corners) of potential niches mark developmental decisions of (or accidental external influences on) an individual. The horizontal axis compresses lifetime niche dimensions onto a single axis. Potential niches can only shrink as individuals commit developmental decisions. The width of the prospective niche at any time point illustrates the potential range of environments (now and in the future) in which an individual has an expected lifetime reproductive success of ≥ 1

its developmental opportunities. The prospective individualized niche is the time-structured space of potential niches.

The prospective individualized niche does not give a lifetime perspective except for the special case of a zygote. Potential individualized niches are affected by previous development (and by accidents). Certain areas of environmental space might not be available if irreversible developmental plasticity in early life-stages prevents an individual from developing a matching phenotype (Nyman et al. 2018). Development has manifest consequences for the individualized niche. The potential niche from a prospective perspective therefore changes as individuals age. In fact, with the possible exception of accidents, it always shrinks, as potentials are widely available at early stages and can only be reduced by individual decisions during development.

The potential time-slice individualized niche, in contrast, might vary across lifetime and might shrink or expand as an individual keeps adjusting its phenotype.

Accidents and 'bad luck' represent a special case that should be taken into consideration. Purely coincidental events that might affect any individual with equal probability shall not be considered as affecting the expectations of lifetime reproductive success. However, not all risks are equally distributed across environments. If individualized niches are unequally risky, then (some) accidents are in fact non-random and genuinely affect fitness expectations. Some individuals may select risky environments with high variance in reproductive success while others select safer environments (Moran et al. 2021). All individuals may have the same probability of being killed by a storm, while choosing to nest in areas with high predator density (or not) affects the reproductive success non-randomly.

However, there is room for a lifelong perspective. We think it is usually meaningless to reconstruct realized individual niches post-mortem for its own sake, since in biology we are rarely interested in unique individuals that represent an ephemeral phenomenon. Rather we aim to understand general patterns and mechanisms. A compilation of individual lifetime niche trajectories (with dynamic changes throughout life) can expose alternative developmental trajectories as bundles of alternative realized niches that change across age (Fig. 5). Such a trajectory-based lifetime perspective helps to answer the question how individualized niches arise during development. We therefore call specific life-history trajectories in environmental space the *trajectory-based individualized niche*.

Definition D: The *prospective individualized niche* is a volume in environmental space in which a particular individual has an expected lifetime reproductive success of ≥ 1 that includes the current and future potential niches. The prospective individualized niche provides a focus on particular developmental decisions, which affect future niche space and can be quantified empirically.

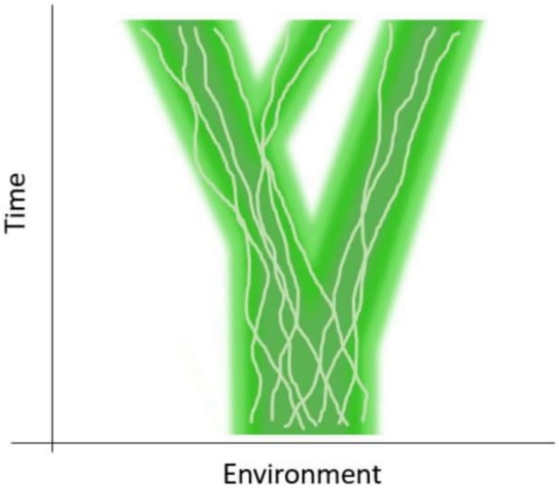

Fig. 5 Schematic view of lifetime trajectory-based niches that emphasize alternative developmental pathways. Light green lines show individual developmental trajectories in niches space. The green background schematically highlights alternative trajectories and switch points that can be identified from bundles of individual developmental trajectories

Definition C: The *time-slice individualized niche* is the environmental space in which a particular individual occurs during a particular part of its development and has an expected lifetime reproductive success of ≥ 1. Aspects of the time-slice individualized niche can be quantified empirically, with repeated measurements.

Definition E: The *trajectory-based individualized niche* is a time-structured volume in environmental space that allows for expected lifetime reproductive success of ≥ 1 and that is different from alternative developmental trajectories. The trajectory-based individualized niche provides a focus on alternative developmental trajectories that affect potential niche space and can be quantified empirically.

The question of dimensions

Hutchinson (1957) defined the ecological niche as an n-dimensional space of environmental dimensions: abiotic (scenopoetic) and biotic (bionomic) factors. Attributes of the focal species, such as specific phenotypes, are not dimensions of the environmental niche. Instead, traits are features that allow a species to occupy a specific environment, for example by providing the ability to exploit particular resource (and traits can be used as proxies for resource use, Roughgarden 1972). Hutchinson distinguished the fundamental niche, the space that can be occupied by a particular species in principle, from the realized niche, the space occupied by a particular population as a consequence of competition. Since the presence of the other species is just a particular dimension of environmental space, the main function of the realized vs. fundamental niche distinction is to highlight how a particular inter-species interaction can affect niche use (a clearly functional perspective). The realized niche is thus the niche of a species in $n - 1$ environmental dimensions.

In analogy to Hutchinson's ecological niche, we define the individualized niche in terms of environmental dimensions, explicitly including all biotic and abiotic factors that are external to an individual. There is no need to restrict the factors to those that are causally relevant to an individual's reproductive success. Some environmental dimensions might have little influence on reproductive success, however this is an empirical finding and should not condition the use of particular environmental dimensions. It is sometimes argued that niche dimensions should be independent, i.e. orthogonal (Blonder et al. 2018). Often they will not be orthogonal and some subspaces will not be realized in any real physical location. It is thus impossible to infer whether some environmental combinations represent part of the niche of an individual (or population). However, it is most useful to define niche space by evidence for presence of an individual rather than lack of evidence for an absence. Combinations of environmental dimensions that are not realized in the real world should thus not be regarded as part of the ecological niche of individuals (or populations). While niche dimensions might not be orthogonal in the real world, it is fair to treat them as orthogonal in hypothetical environmental space.

When scaling down from populations to individuals, the intraspecific context becomes external to the individual. The presence or absence of conspecifics (including potential mates) or conspecifics with particular trait values become an explicit part of the individualized niche. The social context, for example, is part of the individualized niche, like the interspecific community context in the ecological niche of populations. The social conditions that allow an individual to realize a non-zero inclusive fitness are also known as the social niche Blonder et al. 2018; Saltz et al. 2016, see below for a discussion of setting the boundaries). The fact that the intraspecific (including social) context is part of individualized niche dimensions represents one of the most important differences to the population niche. The individualized niche, thus, consists of $n+s$ dimensions, where n represents non-intraspecific dimensions, while s represents the dimensions of the intra-specific niche space (Fig. 6).

The intraspecific context is broader than the social settings. Population density and the frequency of other phenotypes of a species may impact the individualized niche even without social interactions (van Benthem and Wittmann 2020). For example, some prey species such as grasshoppers are color polymorphic (Rowell 1972) and some of their predators develop search images to specialize on the most frequent morph in a population (Bond 2007). The expected lifetime reproductive success of an individual with a particular body color may thus depend on the frequency of that color morph in a population – even if all other environmental variables are identical. Rareness of a particular phenotype can be an advantage even when the phenotype in itself coveys no general benefit (Violle et al. 2017). Such processes give rise to frequency-dependent selection, affecting the niche space of individuals, since some

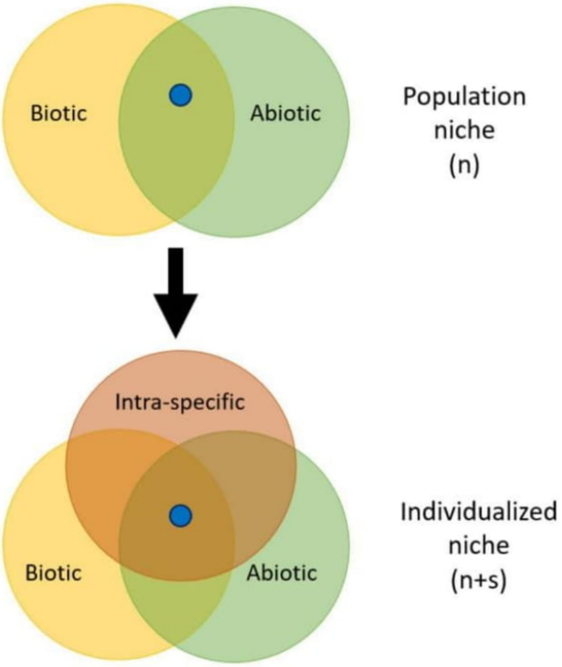

Fig. 6 Dimensionality of the individualized niche. The population niche consists of n dimensions that encompass all environmental conditions under which a population can persist indefinitely. The individualized niche includes all intra-specific dimensions, such as population density and the frequency of alternative phenotypes

phenotypes might be advantageous under some states of the population but not under others.

We suggest that the difference between the presence and absence of intraspecific niche dimensions represents a particularly interesting aspect of the individualized niche, especially since the social environment can have profound influences on later individual phenotypes (Jäger et al. 2019): How does the niche of an individual change in response to the state of the population as a whole (including density and frequency of other phenotypes)? This offers an interesting perspective on the concept of soft vs. hard selection in evolutionary biology (Wallace 1975; Bell et al. 2021). Hard selection refers to selection that is determined by the phenotype of the focal individual and its environment, while soft selection occurs when selection is density- and frequency-dependent. Population density, phenotype frequencies and social interactions are thus important components of the individualized niche.

The question of boundaries

Hutchinson (1957) defined the boundaries of a population's niche by indefinite population persistence and thus non-negative average growth rates in the long term. Population growth rates are determined by the ratio of births to deaths in a population. The equivalent quantities at the level of individuals are survival and reproduction and those can be used for determining the boundaries of individualized niches. However, there are three important considerations, a rather easy and two harder ones, when translating this to the level of individuals.

The easy complication is the question of whether niche boundaries are sharp borders or gradual zones of niche fit. In fact, this consideration applies to both individualized and population niches and can be solved by working with continuous values of population growth rates (in the case of populations) or lifetime reproductive success (in the case of individuals). This results in a nuanced view of core and marginal niche space. A minor complication is that population growth rates and individual lifetime reproductive success are often low under most suitable environmental conditions, especially when they are density-dependent, and the focal population is near its local carrying capacity (Engen and Sæther 2017). This is less of a problem for the individualized niche if population density is considered as one of the niche dimensions. Nevertheless, even in case of the ecological niche of a population, population size (or population density) can be used to estimate the soft borders of niche boundaries.

The harder problem is which concept of individual lifetime reproductive success should be considered. It might be tempting to use realized lifetime reproductive success, quantified in terms of number of offspring produced. However, realized lifetime reproductive success has a large stochastic component and is often a poor indicator of a particular individual's niche fit. If we use the realized lifetime reproductive success (as e.g. Saltz et al. 2016 seem to do), then we do have a problem with individuals that have thrived throughout live, but have bad luck and do not reproduce by some coincidence (see above for a discussion of risk factors). They would be considered to be out of their niche, because their realized lifetime reproductive success (even inclusive realized fitness) is zero. We therefore define the boundaries of individual niche space in terms of expected lifetime reproductive success, which are functions of the phenotype-environment combination (Fig. 7). Expectations of reproductive success do not necessarily invoke propensities in the sense of stochastic dispositions, but are rather built on statistical summaries that follow the law of large numbers (Drouet and Merlin 2015). Individualized niches are thus identified by mapping lifetime reproductive success on phenotype-environment combinations in the form of multidimensional fitness functions. Since there are no replicates of an individual, there is no empirical solution, neither to decompose individual lifetime reproductive success into a stochastic and a deterministic component, nor to quantify individual lifetime reproductive success across different environments. Resorting on fitness components or fitness proxies might be a viable solution (Patrick and Weimerskirch 2014). However, with fitness components we have to abandon (or at least adjust) the absolute threshold of expected lifetime reproductive success of ≥1. Work with fitness components will thus discover mostly gradual (soft) rather than sharp boundaries and this could be done even with relative fitness. Alternatively, we can marginalize across phenotypes (or genotypes) and environments to estimate expected lifetime reproductive success in the form of fitness functions using different individuals as replicates (Fig. 2).

One might wonder whether the boundaries of the individualized niche are defined by a lifetime reproductive success of zero or one (Fig. 7). One problem with repro-

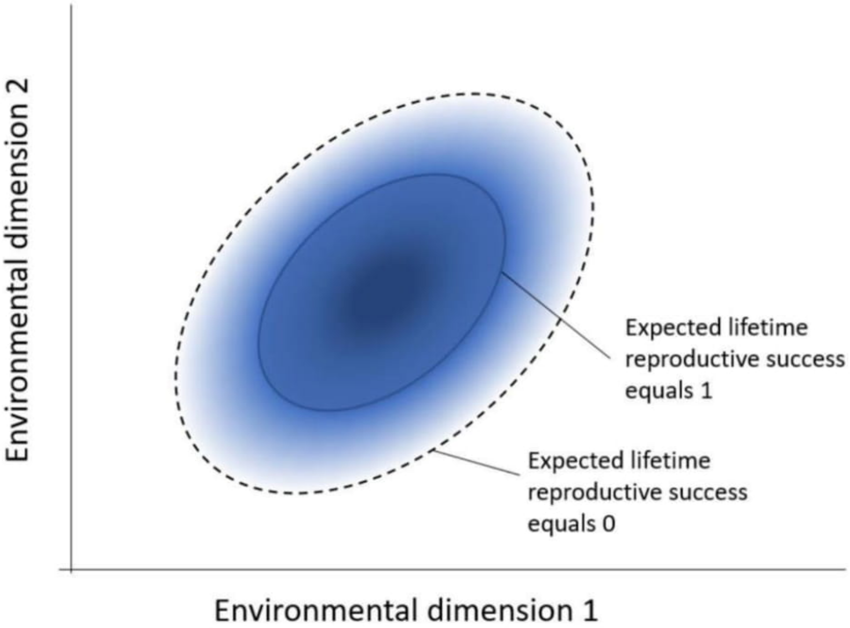

Fig. 7 Multidimensional fitness function and boundaries for the individualized niche. The graded blue area shows the expected (absolute) lifetime reproductive success kernel. The solid blue line marks what we consider the boundary of the individualized niche at an expected isocline of 1. The dashed black line marks the absolute boundary of where expected fitness drops to zero

ductive success expectations is that they might get infinitely small and it might be difficult to tell where they become zero. The condition of (simply) positive reproductive success expectations thus forms a theoretical boundary that is difficult to determine empirically. We argue that while individuals cannot persist indefinitely, they need to leave at least one offspring to perpetuate into future generations. A useful threshold for the boundary of the individualized niches is thus the (long-term) expectation to produce one descendant. We think that this makes a useful benchmark in a gradual view of the individualized niche.

Conclusions

We have started with a discussion of individual differences in behavior. We now want to come back to this and ask whether individualized niches are a mere rebranding of the study of individual differences. In brief, we think there are important differences. First, in our concept it is not the phenotype itself that represents the individualized niche, but the environment that an individual lives in. Not all individual differences in phenotype and behavior are thus relevant to the individualized niche (Trappes et al. 2021). The subset of individual differences, which mediates phenotype-environment matches (Edelaar and Bolnick 2019), is the most relevant to the individualized niche. While the literature on individual differences focuses mainly on survival and fitness consequences of individuals, the individualized niche focuses on the environment and, in particular, relates the phenotype-environment match to individual differences (in line with Roughgarden 1972). Furthermore, in order to estimate individualized niches, the full range of an individual's ecology and life history needs to be studied. This highlights the urge for studies, which incorporate lifetime-long observations of individuals.

We have introduced the field of animal personality and the ecological niche concept and have discussed how they can merged into the concept of an individualized niche. We provide a working definition of individualized niche that builds on Hutchinson's population-level ecological niche. However, there are important intricacies when developing an individualized niche concept. Particularly important are (i) the differentiation between realized and potential niches where the latter is defined by unobservable outcomes, (ii) the dynamic nature of individualized niches with a time-slice, a prospective and a trajectory-based perspective, (iii) the inclusion of intra-specific dimensions in the dimensionality of individualized niches and (iv) the need to define the boundaries of individualized niche space by expected lifetime reproductive success (not realized lifetime reproductive success). We hope that these considerations will help other scientists to further develop the concept of the individualized niche into a practicable tool for empirical studies and conceptual progress.

There are important challenges in applications of the individualized niche concept. One of them is the efficient identification of relevant niche axis. While the niche in itself is highly multidimensional, there are likely a few important niche dimensions that matter the most, when explaining individual differences. Therefore, the challenge for practitioners will be to find ways to reduce the dimensions of individualized niches to those variables, which are important for individuals. The second challenge is the efficient use of statistical models to predict fitness expectations. Nonlinearities and interactions complicate the prediction of fitness expectation (and any marginalization across individuals), so that the functional relationships need to be sufficiently well known. Linear prediction and simple (additive or multiplicative) interactions might be the first approximations in practice, but are likely overly simplified. The third challenge is the efficient use of good proxies of lifetime reproductive success in cases where it cannot be determined directly.

While we see our concept mostly of a metaphorical value, we also think it has practical implications. As a metaphorical concept, it can provide thinking aids for new scientific avenues. Importantly, we provide subcategories of the concept that, we think, may help to distinguish features that are sometimes treated under the term 'individualized niche'. We thus bring structure to the concept. We also provide practical advice on empirical quantification of the individualized niche. The realized and the trajectory-based individualized niches can be quantified quite directly, via repeated observations of the same individuals. The time-slice niche is already often quantified, in many animal personality studies, though a stronger focus on individualized phenotype-environment matches is desirable. The prospective niche can be quantified empirically by focusing on the consequences of developmental switch-points and might even provide fresh perspectives on animal behavior. The potential individualized niche is the most complicated to be measured empirically and requires some grouping of individuals with similar phenotypes, but still provides more detailed perspective of the ecological niches than Hutchinson's population niche. We hope that the individualized niche, in its different flavors, allows a more informative view of what is often treated as the niches of the population. Individuals differ and this often has ecological and evolutionary consequences. The main challenge will be the identification (and quantification) of relevant niche dimensions within the full niche space, which is characterized by high dimensionality.

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Manuscript 3

Novelty at second glance: a critical appraisal of the novel object paradigm based on meta-analysis

Elina Takola, E. Tobias Krause, Caroline Müller, Holger Schielzeth

Animal Behaviour (2021)

Data and code available in: https://github.com/ETakola/NoveltyAt2ndGlance

The great tit (Parus major) is one of
the most popular species in novel object studies.
© Elina Takola

FORM 1

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Authors' contributions (in %) to the given categories of the publication

Author	**Conceptual**	**Data analysis**	**Writing the manuscript**
Elina Takola	70%	70%	70%
Holger Schielzeth	20%	30%	20%
E. Tobias Krause	5%	0%	5%
Caroline Müller	5%	0%	5%
Total:	100%	100%	100%

______________________ ____

Signature candidate

Signature supervisor (member of the Faculty)

“Inadvertently, I had stumbled across what has been called
the Harvard law of animal behavior, which is related to Murphy's law:
You can have the most beautifully designed experiment with the most carefully
controlled variables, and the animal will do what it damn well pleases.”
(Ehrenreich 2018)

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Novelty at second glance: a critical appraisal of the novel object paradigm based on meta-analysis

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The study of consistent individual differences has become an important focus in research on animal behaviour. These behavioural differences are typically measured through standardized testing procedures. One frequently used paradigm is the novel object test, in which animals are exposed to unfamiliar objects and their reaction is quantified. We used meta-analysis to evaluate how reliably novel object trials quantify individual differences. Overall, we found repeatability of responses to novel objects was strong and significant and was larger in short-term than in long-term studies. Average sample size and long-term estimates have both increased over the past three decades. Most short-term studies used different novel objects in repeated presentations, while long-term studies used either the same or different novel objects almost equally often. Novelty, the time interval between trials and their interaction together explained little of the total heterogeneity, while between-study heterogeneity remained large. Overall, novel object trials reliably estimate individual differences in behaviour, but results were very heterogeneous even within the same study species, suggesting susceptibility to unknown details in test conditions. Most studies that use novel object trials in a foraging context label the trait as neophobia, while novel object trials in a neutral context are labelled variously as shyness–boldness, exploration–avoidance or neophilia. To avoid ambiguity, we argue for the use of object–neophobia for trials near resources and object–neophilia for trials in a neutral context as the most specific labels for novel object responses.

Consistent individual differences in behaviour are widespread in nature. For a long time, individual differences were considered noise around an optimum niche value, but nowadays it is well established that intraspecific variation is of adaptive importance and can affect reproductive success (Smith & Blumstein, 2008), growth rates (Royauté et al., 2018), metabolic rates (Holtmann et al., 2016) and even population dynamics (Levin et al., 2000). It has also been shown that individual differences in behaviour have a heritable basis (Dochtermann et al., 2015; Stirling et al., 2002) and hence can evolve by natural selection. The study of individual differences has therefore become an important topic in behavioural ecology.

Temporally consistent individual differences in behaviour that are correlated across contexts are variously called animal personalities, behavioural syndromes, coping styles or temperament (Réale et al., 2007). We here refer to them as animal personalities without prejudice towards other terms. One hallmark of animal personality is that individual differences are stable over time (Kaiser & Müller, 2021; Sih et al., 2004). Most empirical studies on animal personality use standardized experimental set-ups with repeated measurements per individual to quantify temporal consistency. It is therefore important to evaluate the suitability of standardized experimental set-ups for the quantification of individual differences. We here focus on reliability of a specific testing paradigm, the novel object test (Yerkes & Yerkes, 1936), and evaluate sources of heterogeneity in study outcomes.

Novel object trials have become popular in recent years. In these trials, animals encounter an item that they had never seen before (thus a novel object) and their behavioural responses are quantified, often as approach latencies or approach distances (Greenberg, 1990; Guenther & Brust, 2017; Yerkes & Yerkes, 1936). Novel object trials are mostly used to quantify shyness–boldness, exploration–avoidance or

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neophilia/neophobia. Shyness–boldness and exploration–avoidance are generally seen as major axes of continuous personality types (which we indicate by the en dash Réale et al., 2007). It is less clear whether neophobia/neophilia represent the same or different personality axes (Mettke-Hofmann, 2014; Mettke-Hofmann et al., 2002) indicated by the slash. Variants of novel object trials aim to separate neophilia and neophobia by varying the context of testing in placing a novel object either in a neutral position (for neophilia) or close to an essential resource such as food for a quantification of neophobia (Greggor et al., 2015).

Shyness–boldness describes an animal's behaviour in a risky but not necessarily novel situation (Réale et al., 2007). Exploration–avoidance refers to the exploration of explicitly novel situations and is often used in a spatial exploration context (Réale et al., 2007). Neophobia/neophilia refer to responses to novelty per se and are sometimes considered as components of exploration–avoidance (Réale et al., 2007). The novel object test is not the only testing paradigm to measure shyness–boldness, exploration–avoidance or neophilia/neophobia. Shyness–boldness is also often quantified by startle response trials, emergence from shelter, response to predator (cues) or by mirror image trials (Ioannou et al., 2008; Noer et al., 2015). Exploratory behaviour is also often quantified by open field or novel-environment trials. Neophilia/neophobia is a more specific term to novel object trials, although it is sometimes also used for novel environment trials (Greggor et al., 2015). Mettke-Hofmann (2012), therefore, proposed to distinguish object neophilia/neophobia for novel object trials from spatial neophilia/neophobia for novel-environment trials.

Independent of the question of labelling is the question of repeated presentations and how they should be best embedded in the experimental design. While the first presentation of a novel object can generate the intended response, upon second presentation of the same item, objects are no longer novel. The second presentation may thus trigger a reduced behavioural response (Berlyne, 1966). The alternative is to use different unfamiliar objects, although these might trigger different responses if, for example, they differ in conspicuousness or perceived riskiness. Greggor et al. (2016) suggested that objects should be used that differ slightly but clearly. However, similarity and differences are ambiguous categories and what might be perceived as similar by some might be seen as different by other individuals. Furthermore, some species might habituate to novel stimuli per se (Réale et al., 2007), such that different novel objects do not trigger the same behavioural response upon second presentation.

The effect of using the same or different objects in repeated trials likely depends on the time interval between repeats. The degree of novelty in these repeated trials is the result of perception and memory and thus depends on the cognitive ability of individuals (Mettke-Hofmann, 2014), but our understanding of animal memory and cognition mechanisms is still incomplete, in particular when it comes to a large range of taxa. It is likely that the effects of novel objects differ between short-term replication (within hours, days or weeks) and long-term replication (after months or years). Therefore, the time interval between trials should be considered when assessing the role of the same or different objects in novel object trials.

We here review the reliability of the novel object paradigm using meta-analytic techniques (Gurevitch et al., 2018; Koricheva et al., 2013). Meta-analysis is a powerful tool for research synthesis in science, as it provides an objective and replicable quantitative overview of literature. Although a common criticism of meta-analytic methods highlights the pooling of incomparable effect sizes (also known as 'apples and oranges problem'), we address the issue of diverse study designs by adding variables as moderators, i.e. the equivalent to covariates in regression models, in meta-regression models, and accounting for multilevel heterogeneity. The use of moderators as fixed effects allows for the identification of context dependencies (such as testing context, wild versus captive populations, etc.) that affect the magnitude of individual differences. Moreover, we account for phylogenetic correlations, since closely related species might react similarly to the same stimuli (Nakagawa & Santos, 2012). Thus, we are able to explore the impact of various effects on the consistency of behavioural traits from multiple studies.

Besides the synthesis of effect sizes by meta-analysis, we present an overview of the most common terms used to describe the measured behaviours. We do not aim to take a stance on the validity of novel object trials to measure these traits, particularly since validity might differ between study systems. We rather aim to summarize how novel object responses are typically labelled in the published literature. By doing so, we take a phenotype-based approach that focuses on behaviour rather than on the underlying emotional, neurological and hormonal processes. We acknowledge that it would be desirable for the field to gain an in-depth process-based understanding for all study systems.

The main aim of our meta-analysis is to evaluate the reliability of the novel object test in quantifying individual differences in behaviour. We do so by conducting a meta-analysis of the magnitude of the correlation between repeated novel object trials, as well as testing context dependencies by moderator and subset analyses. Specifically, we test for (1) the dependency of the correlation on the time gap between measurements, (2) the effect of using the same or different objects during repeated novel object trials and (3) the effect of placing the object in a neutral context or next to a valuable resource (food or nest). Furthermore, we explore other sources of heterogeneity, such as differences between wild and captive individuals, as well as how the use of novel objects has changed over time in terms of sample sizes. Finally, we summarize and discuss variation in terminology when labelling response behaviours and present an overview of the most common response behaviours quantified in novel object trials.

METHODS

We used systematic reviewing techniques to evaluate the properties of the novel object paradigm for quantifying consistent individual differences in behaviour (Koricheva et al., 2013). Our methodology followed the preferred reporting items for systematic reviews and meta-analyses protocol (PRISMA), which aims to increase the robustness of meta-analyses and is based on a checklist (Moher et al., 2009).

Data Collection

We conducted a search in the Web of Science (WoS) Core Collection 5.24. The query included not only the term novel object (novel object*), but also words related to behavioural phenotypes (e.g. neophob*, neophil*, bold*, shy*) and the time range was set to 1990–2020 (see Appendix). The early 1990s were the time when novel object trials were first used systematically to quantify individual differences for context-general behavioural traits (Greenberg, 1990). We also initially searched for the term explorat*, but the number of hits was very large (more than 3000 additional publications). Thus, we used, instead, the combination explorat* and object*, which resulted in 572 additional publications. The WoS Category was limited to Behavioural Sciences and duplicates were removed, resulting in 3984 publications that were used for more detailed screening. The literature search was finalized on 15 March 2021.

Inclusion and Exclusion Criteria

We searched for empirical studies that used novel object trials and quantified the responses of individual animals to these objects.

A novel object should be unfamiliar to focal animals so that we do not expect an evolved attraction to these objects; we thus excluded objects that represent food resources of a species. We did include novel food sources in our analysis if the novel food was sufficiently different from the natural food of a species. This included studies that use artificial dyes to stain natural food if the novel food colour was considered sufficiently novel and unusual.

We screened studies based on the following criteria (Appendix Table A1). First, studies should be done with outbred, nonhuman animals with unimpaired physical condition. Second, studies should use a novel object paradigm, thus excluding presentations of mirror images, live conspecifics, taxidermy mount presentations and food resources of a species. Third, studies should have repeated novel object trials using focal individuals. Fourth, studies should report relevant correlations or repeatability as a measure of individual consistency.

We conducted the screening process in two stages. We first screened titles and abstracts, which excluded 3172 publications, mostly because they did not represent empirical studies, they were done on humans, they did not use systematic novel object trials or they did not study individual differences (Fig. 1). Only clearly nonfitting cases were excluded during abstract screening and ambiguous cases were taken forward to the next step. We next screened full texts of the remaining 812 publications. Screening of full texts was done independently by two people (E.T. and H.S.) and conflicts (10%) were resolved jointly. Full-text screening was focused on the same general criteria and on whether relevant effect and sample sizes were reported. Another 697 publications were excluded during full-text screening (Fig. 1). One study was opportunistically added to the final data set (see Appendix). Consequently, 115 studies matched our inclusion criteria and generated 265 effect sizes.

Data Extraction

We extracted pairwise correlation coefficients (Pearson, Spearman or Kendall) and repeatabilities (R or ICC), as we were interested in the temporal consistency of behavioural responses between trials. Effect sizes typically corresponded to two rounds of novel object trials with the same set of individuals. In cases where more than two rounds of testing were conducted or when multiple responses were quantified, multiple effect sizes were extracted from one study. When combined repeatabilities were reported for more than two trials, we extracted these repeatabilities as the relevant effect sizes. In five cases correlation measures were extracted from graphs using the metaDigitise package, version 1.0.1 (Pick et al., 2019).

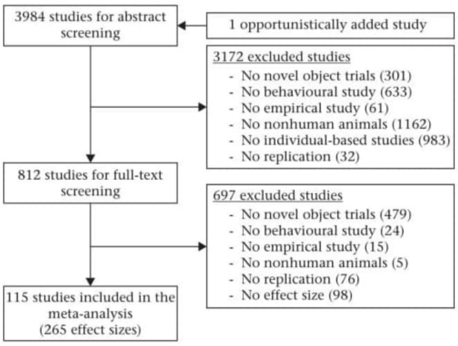

Figure 1. PRISMA diagram with abstract and full-text screening results. Numbers show the number of publications that were excluded or included.

For each effect size we extracted information related to (1) publication (year, authors and journal), (2) animals tested (species, sample size and domestication status), (3) testing conditions (novelty of the object in the repeated trials, time interval between trials and context of testing), (4) response behaviour being quantified (specific individual behaviours, response type, see below), (5) analyses being conducted (whether multiple personality traits were assayed, whether repeatabilities were calculated from non-Gaussian generalized linear models) and (6) the terms used to describe the behavioural phenotype (see Appendix Tables A2 and A3 for a detailed description).

The novelty of the object in repeated trials was a parameter of key interest in our analysis. When the novel objects were the same but of different colours, we considered them as different objects. Context of testing was categorized into (1) novel object in neutral position, (2) novel object close to food or (3) novel object close to nest. For domestication status we distinguished between (1) domestic animals tested in an artificial environment, (2) laboratory-reared animals tested in an artificial environment, (3) wild-caught animals tested in an artificial environment and (4) wild animals tested in a natural environment (Mathot et al., 2019). Regarding the response type and behaviour, we recorded the specific trait being quantified (if it was a single behavioural response), whether the response was a composite of multiple behaviours within the same trial (often principal component scores of multiple behaviours scored within the same trial or other synthetic response scores based on multiple components of behaviour) or whether the response was an average calculated across multiple (sub)trials. We did not record transformations being used, since we consider this a decision of individual researchers to best quantify the behaviour, similar to the researcher's decision to record a specific response behaviour and not another. For the same reason, we also did not distinguish between parametric (Pearson) and nonparametric (Spearman or Kendall) correlations. However, 10 studies analysed behavioural phenotypes as binary responses or using Poisson models, and these might produce systematically lower consistency measures; the type of model was therefore recorded.

The time interval was recorded in days, assuming 30 days in a month and 365 days in a year when converting from descriptions in publications. Since our data set included many species with different life histories, we also tried to standardize time intervals by dividing them by the species' life span (compiled from the AnAge database; Tacutu et al., 2018) to express the time interval as a proportion of life span. However, raw time interval measures and lifetime standardized measures were highly correlated ($r = 0.94$), and results were qualitatively unaffected, such that we used log-transformed time interval in days as a moderator in our analysis.

Effect Size and Weighting in Meta-analytic Models

We used R 3.6.3 for all analyses (R Core Team, 2020). Correlation and repeatability measures were transformed using Fisher's Z-transformation as implemented in the escalc function of the metafor package, ver. 2.4.0 (Viechtbauer, 2010). Since we dealt with pairs of observations, correlations and repeatabilities are equivalent; thus, when transformed back, we used r to indicate both. Effect sizes were weighted by the inverse of sampling variance in all analyses. We extracted multiple effect sizes from some studies and therefore it was possible to estimate heterogeneity (variability) across effect sizes (within-study) as well as between studies, species, etc (see below).

Meta-Analyses and Meta-regressions

We conducted a phylogenetic multilevel meta-analysis to estimate the overall effect. Phylogenetic information was downloaded from Open Tree of Life version ott3.2 (Hinchliff et al., 2015) using the rotl (ver. 3.0.11) R package (Michonneau et al., 2016). After constructing an ultrametric phylogenetic tree (Appendix Fig. A1) using the Grafen (1989) method, we converted the tree to a correlation matrix. This matrix was fitted as a random effect in our meta-analytic model, along with random effects for effect size ID, study ID and species ID. The analysis was performed first using the complete data set and then separately for major taxonomic groups (mammals, birds, fish, reptiles and insects). Weighted random-effect-only meta-analytic models were fitted using the rma function of the metafor package.

Besides the random-effect-only meta-analytic model, we also fitted a meta-regression with moderators (Appendix Table A3), once for the complete data set and once for every major taxonomic group represented by more than 10 publications in our data set (mammals and birds). As moderators we fitted the time interval between repeated trials (log-transformed), novelty (two levels), domestication status (four levels), correlation type (two levels), a binary indicator for non-Gaussian linear models, a binary indicator of whether multiple behavioural tests were performed in the study (other than the novel object), response type (three levels), testing context (three levels) and the interaction of novelty with time interval. The meta-regression models with moderators were also fitted for subsets of the testing context (neutral, food, nest) separately. As above, the random effects of the meta-regression were the effect size ID, study ID, phylogeny and species.

Heterogeneity (I^2) was examined for multiple levels in every model in our meta-analysis, including the subsets of different clades (Nakagawa & Santos, 2012). We also calculated marginal R^2 to estimate the proportion of variance explained by fixed effects (Nakagawa & Schielzeth, 2013). The variance explained by individual predictors was calculated by fitting only the predictor of interest (along with the random components) in a meta-regression model, followed by calculation of marginal R^2. We also calculated τ^2, which reflects true heterogeneity, as it is the measure of variation among effects observed in different studies.

Sensitivity Analyses

We conducted influence diagnostics and sensitivity analyses to evaluate the robustness of our results. For the influence diagnostics we used the influence function of the metafor package, version 2.4.0 (Viechtbauer, 2010), to identify influential studies using Cook's distance and the rstudent test. The diagnostics showed five potential outliers in the data set (Appendix Fig. A2). We therefore refitted the meta-analytic model again while excluding the five influential effect sizes. Since the overall estimate was not significantly affected, we present the analysis of the full data set.

Publication Bias

We tested for publication bias qualitatively through visual inspection of funnel plots and quantitatively by Egger's regression (Egger et al., 1997). Funnel plots were generated by plotting effect sizes against inverse sampling variance and inverse standard error. Egger's regression estimates funnel plot asymmetry as an indicator of publication bias. In addition, we examined the possibility of time lag bias, which is the decrease in effect sizes with increasing year of publication (Trikalinos & Ioannidis, 2006). The test for differences in effect sizes between studies that used novel object trials as the only personality-scoring paradigm versus studies that used multiple measures of personality traits also served as a test for publication bias. We expect studies with a single behavioural measure to be more likely to report statistically significant temporal consistency than studies that report multiple behavioural traits, out of which only a subset might be significantly repeatable.

RESULTS

Screening of 3984 abstracts and full texts resulted in 289 studies that used novel object trials to quantify individual behaviour in nonhuman animals. Of these studies, 213 (74%) replicated novel object trials for all or for a subset of individuals. After excluding 98 studies with repeated novel object trials that did not allow an extraction of effect sizes for temporal consistency, we found 265 effect sizes from 115 studies (Fig. 1) to be included in the analyses. This data set encompassed 70 species (22 mammal, 35 bird, five fish, four reptile and four insect species; Appendix Fig. A1).

Testing Practices

Sample size ranged from five to 567 individuals per effect size estimate (mean ± SD: 47.7 ± 57.6) and increased significantly by about 2.3% per year (effect of year of publication on log(N) sample size: $b = 0.023 \pm 0.008$, $t_{192} = 2.84$, $P = 0.005$; Fig. 2).

The time interval between two consecutive trials ranged between a few hours and 4 years (<0.1%–82% when expressed relative to the expected life span of the focal species). Seventy-two effect sizes (27%) refer to trials repeated on the same (eight effect sizes) or on consecutive days (64 effect sizes). Of the effect sizes, 62% were calculated from replications after at least 1 week, 42% after more than 1 month and 11% after at least 1 year. Studies over longer time periods became more popular over the years with an increase in the time interval between trials of about 14% per year (effect of year of publication on log(time interval): $b = 0.139 \pm 0.023$, $t_{192} = 6.08$, $P < 10^{-5}$; Fig. 2). In the following, we operationally define effect sizes calculated from repeats less than 1 month apart as short-term replications and those with longer intervals as long-term replications.

Seventy-five studies used different objects in repeated trials, 33 used the same objects and seven used both. Most short-term studies (83% of effect sizes for short-term repeatabilities) used different objects, while the same 'novel' objects were used more often when addressing long-term consistencies (only 34% different objects among estimates for long-term repeatabilities; Appendix Table A2). Domestic animals were represented by 40 effect sizes (15%), laboratory-reared animals accounted for 42%, wild-caught animals for 29% and wild animals tested in the wild only 14%.

Eighty-two studies conducted novel object trials in a neutral context (74% of effect sizes), 30 next to a food source (20% of effect sizes) and nine inside or close to the nest (5.6% of effect sizes). Most studies calculated individual consistencies for a specific response behaviour (76% of effect sizes), while some used principal component or other composite scores calculated from multiple behavioural components measured in the same trial (12% of effect sizes) or calculated individual temporal consistencies after averaging across multiple trials (12% of effect sizes). Most studies (86%) used novel object trials along with other standardized personality assays (such as open field trials, startle responses or intruder trials), while only 16 studies (14%) focused on the behavioural consistency for novel object trials only (Appendix Table A2).

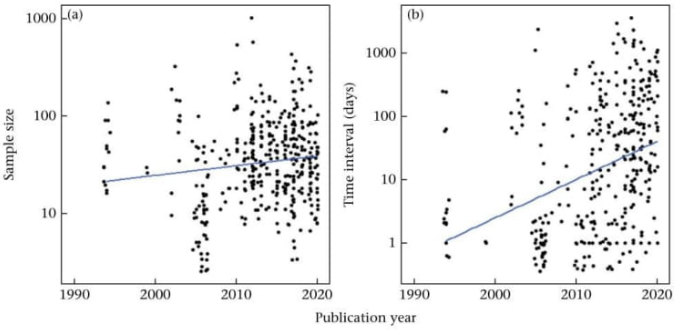

Figure 2. Temporal trends of (a) sample size and (b) time interval between repeated trials. Black dots show raw values of sample sizes and time intervals. The sample size and time interval are shown on a log scale.

Overall Effect Sizes and Heterogeneities

The overall effect of the phylogenetically controlled meta-analysis was strong and significantly greater than zero ($\beta_0 = 0.52$, confidence interval, CI = [0.46, 0.57]), which is equivalent to a correlation of $r = 0.47$. Heterogeneity among effect sizes was high ($I^2_{\text{total}} = 80\%$). Variation among studies and among effect sizes accounted for 54% and 25% of this heterogeneity, respectively, while species identity and phylogenetic relationships explained a negligible part. The average short-term repeatability was $r = 0.52$ (equally for time intervals up to 1 week and for time intervals between 1 week and 1 month; Fig. 3), while the average long-term repeatability was $r = 0.40$ ($r = 0.41$ for time intervals of 1 month to 1 year and $r = 0.39$ for time intervals of more than 1 year).

We repeated the analysis separately for the subsets of mammals, birds, fish, reptiles and insects. Mammals, bird, fish and insects showed strong and significant consistencies of behaviour (all $r > 0.40$), while individual consistency was low and nonsignificant for reptiles ($r = 0.074$; Table 1). Total heterogeneity was particularly high in the subsets of mammals, birds and fish (all $I^2_{\text{total}} > 80\%$), but not for insects and reptiles ($I^2_{\text{total}} < 4\%$; Table 2). Between-study heterogeneity was particularly high for the subset of mammals and fish ($I^2_{\text{study}} > 62\%$), moderate for birds ($I^2_{\text{study}} = 32\%$) and low for insects and reptiles (Table 2). The amount of real heterogeneity, expressed by tau-squared, was $\tau^2 = 0.078$, CI = [0.07, 0.11].

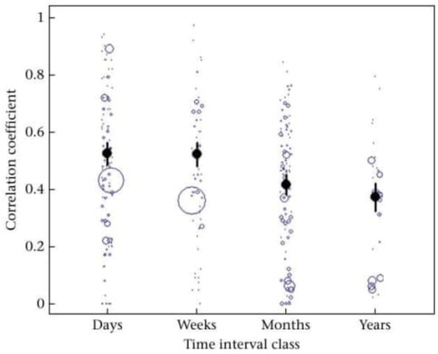

Figure 3. Correlation coefficients for four classes of time intervals between repeated trials. Open dots show correlation coefficients (dot size scaled by sample size) and black dots and bars show random-effect-only meta-analytic model estimates ± SE. Days = 0–6 days, weeks = 7–30 days, months = 31–364 days, years = 365 + days.

We also fitted the meta-analytic model for each subset of testing context (neutral, food, nest). When the object was placed in a neutral position repeatability was $r = 0.46$, whereas when it was placed close to food or the nest repeatabilities were higher ($r = 0.55$ and $r = 0.53$, respectively). However, the large estimate for objects close to the nest was partly caused by a larger proportion of short-term studies (nine of 15 effect sizes) in this subset.

The Impact of Novelty and Time Interval

The amount of total heterogeneity in overall effect indicated scope for effects of moderators. We therefore fitted a meta-regression with novelty, time and their interaction as moderators. This meta-regression was first fitted for the full data set and then for the subsets of taxa with >10 studies (i.e. mammals and birds). The moderators explained in total 3% of the variance and did not have a significant effect on the correlation ($Q_M = 5.35$, $P = 0.15$). Novelty had a low and nonsignificant effect on behavioural consistency and, as expected, time yielded a negative estimate (shorter time intervals resulted in higher repeatability estimates). The estimate for the interaction was negative (the effect of time interval was stronger if objects were different), but not significantly different from zero ($\beta_{\text{int}} = -0.0001$, CI = [−0.0414, 0.0412], $P = 0.92$). Similar trends were observed in the subsets of mammals and birds (Fig. 4). In the overall model and the subset of birds, these moderators explained around 4%, but in the subset of mammals, they explained 7%. Even though meta-regression did not show a significant effect of time, long-term consistencies seem to be markedly lower than short-term consistencies when the data are broken down to time interval classes (Fig. 3).

The Impact of Other Moderators

We explored effects of additional moderators in the meta-regression model by fitting each of them in a meta-regression model. As for novelty and time interval, we fitted these meta-regressions once for the whole data set and once for each taxon with >10 studies (i.e. mammals and birds). Domestication status accounted for a low fraction of variance ($R^2_{\text{dom}} = 1\%$) and was not significantly correlated with the overall effect size. In the subset of mammals, domestication status explained 2% of variation and for birds 1%. However, the levels of domestication status did not show consistent estimates across different subsets of the data (Fig. 4).

Table 1
Summaries and results from phylogenetic multilevel meta-analyses

	$N_{E.S.}$	$N_{studies}$	$N_{species}$	Zr	SE	LCI	UCI	z	P	r
Overall	265	115	70	0.52	0.03	0.46	0.57	17.37	<0.0001	0.47
Mammals	93	36	22	0.54	0.05	0.43	0.65	9.69	<0.0001	0.49
Birds	141	62	35	0.54	0.042	0.46	0.62	12.75	<0.0001	0.49
Fish	19	10	5	0.52	0.15	0.22	0.81	3.43	<0.001	0.46
Reptiles	8	3	4	0.07	0.05	−0.02	0.17	1.49	0.17	0.074
Insects	4	4	4	0.43	0.07	0.28	0.58	5.70	<0.0001	0.40

LCI and UCI indicate the lower and upper limits of the 95% confidence intervals; $N_{E.S.}$ indicates the number of effect sizes; $N_{studies}$ indicates the number of studies; $N_{species}$ indicates the number of species; Zr indicates the Z-transformed correlation calculated by the meta-analytic model; r indicates the correlation (back-transformed) calculated by the meta-analytic model.

Table 2
Total heterogeneity in effect sizes (%) across hierarchical levels of random effects for the overall data set and for subsets of the data

	$I^2_{species}$	I^2_{phylo}	I^2_{study}	$I^2_{e.s.}$	I^2_{total}
Overall	0	0	54	26	80
Mammals	0	0	62	19	81
Birds	6.2	6.2	32	35	80
Fish	0.1	0.1	73	7	80
Reptiles	0	0	4	0	4
Insects	0	0	0	0	0

Accuracy is given to one decimal only for effects <10%. $I^2_{species}$ indicates the heterogeneity observed at the level of species; I^2_{phylo} indicates the heterogeneity observed at the level of phylogeny; I^2_{study} indicates the heterogeneity observed at the level of study ID; $I^2_{e.s.}$ indicates the heterogeneity observed at the level of effect size ID; I^2_{total} indicates the total heterogeneity.

Testing context explained only 1% of the total heterogeneity. The type of response (single behaviours, aggregates of multiple components and averages across trials) had no significant effect and the effect of estimation by non-Gaussian models was also nonsignificant. All moderators explained less than 4% in all cases except in the subset of mammals in which the response type explained 11%.

Publication Bias and Sensitivity Analysis

For sensitivity analysis, we refitted the overall meta-analytic model without five particularly influential studies (Appendix Fig. A2). The estimate of the overall effect marginally decreased from $\beta_0 = 0.52$ to 0.49 (CI = [0.44, 0.54]), whereas the total heterogeneity dropped from 80% to 72%.

Visual inspection of the funnel plot showed only weak asymmetry of effect sizes (Fig. 5). However, Egger's test identified significant asymmetry ($t_{199} = 3.04$, $P = 0.003$) but a subsequent trim-and-fill method estimated zero missing effect sizes. We tested for time lag bias by fitting a meta-regression with publication year as a predictor. The slope showed a negative trend ($\beta = -0.02$, CI = [−0.04, 0.0036], $Q_M = 5.41$, $P = 0.02$) which explained 3.5% of variance. Studies that reported multiple behavioural traits had nonsignificantly larger consistency estimates than studies that focused on novel object trials. This result is thus not indicative of publication bias.

Reproducibility Within Species

The amount of heterogeneity explained by species was estimated to be zero in the overall meta-analysis. However, most species were used only in one or a few studies. Three species, though,

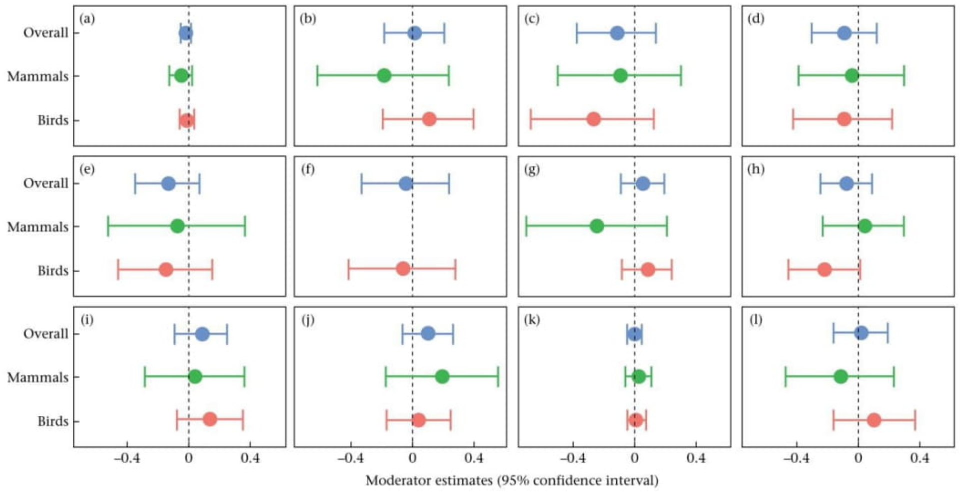

Figure 4. Forest plot showing the results of meta-regressions using the full data set and subsets of bird and mammal species. Moderators were (a) time interval, (b) novelty, (c), (d), (e) the domestication gradient of testing and (f), (g) testing context (position of novel object relative to resources), (h) non-Gaussian models, (i) PCA scores, (j) composite measures of behaviour, (k) the interaction of novelty and time and (l) multiple behavioural assays during the study. The reference category combination in the model was the same object, wild-caught animals tested in the wild, neutral context, Gaussian models, single behaviour, repeatability estimate and only novel objects as the only personality trait being assayed.

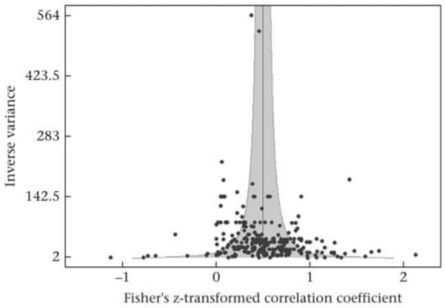

Figure 5. Funnel plot of inverse sampling variation against effect sizes for an assessment of publication bias.

were used in more than three studies, so we inspected the consistency of estimates within these species (guinea pig, *Cavia aperea*, zebra finch, *Taeniopygia guttata* and great tit, *Parus major*) more closely. Estimates of individual consistency in response to novelty of the guinea pig were done with two laboratory populations (domestic guinea pigs and wild-derived cavies) in the same research laboratory, all with the novel object in a neutral context and they used either latency to approach or the number of touches as a response. Nevertheless, estimates varied widely (Fig. 6). Estimates with zebra finches were all done in seven different outbred captive laboratory populations (including the study with the second largest sample size in our data set) and were performed either in a neutral context or close to food. Estimates varied widely (Fig. 6) within contexts and even within the same population with multiple estimates. Estimates for the great tit were particularly heterogeneous in context (neutral, near food or near nest) and they were conducted in the wild, in the laboratory with wild-caught birds or with laboratory-bred individuals. However, the scatter of estimates was similar to the cases of guinea pigs and zebra finches (Fig. 6).

Terminology

Most studies (48 studies, 42%) labelled responses to novel objects as either neophobia (38 studies, 32%), neophilia (10 studies, 9%), shyness–boldness (31 studies, 27%) or exploration–avoidance (22 studies, 19%), while more rarely occurring labels were fearfulness (five studies), approach–avoidance (two), risk responsiveness (two) and activity (one) (Appendix Tables A4–A6). Eight studies did not use any general labels for the traits being measured. Labelling was associated with testing context, with an even stronger bias towards neophobia when novel objects were placed next to food or nests (70% across these two contexts) and a more even distribution across neophobia/neophilia, shyness–boldness and exploration–avoidance when the novel object was in a neutral place (Appendix Table A4, Fig. A3).

DISCUSSION

Our meta-analysis of individual temporal consistencies, as quantified in novel object trials, revealed an overall strong and significant repeatability in responses to novel objects ($r = 0.47$). This estimate is substantially larger than an estimate of average repeatability in behaviour, $r = 0.37$ (Bell et al., 2009), which demonstrates that the novel object paradigm is a useful and reliable way to quantify consistent individual differences between individuals. The long-term repeatability was overall lower than the short-term repeatability. Any state-dependent causes of individual differences are likely to be temporally autocorrelated, such that short-term repeatabilities are expected to be higher than long-term repeatabilities. Furthermore, environmental variables also tend to be temporally autocorrelated, which can lead to pseudorepeatability, in particular when individuals select their different microenvironments or individualized niches (resulting in 'recurrent environments'; Dupré, 2014). Environmental autocorrelation is likely to affect short-term repeatabilities more strongly than longer-term repeatabilities.

General Evaluation of the Novel Object Paradigm

The rather high overall repeatability in response to novel objects shows that novel object trials provide a generally suitable paradigm for the quantification of temporal consistencies and behavioural differences between individuals. However, we found substantial heterogeneity in effect sizes, mostly between studies and to a lesser degree between species. The large heterogeneity poses the question of whether differences between studies reflect genuine differences between populations or whether they reflect differences in the uncontrolled aspects of the experimental set-up. There are many reasons why populations may differ in the relative magnitude of individual differences. For example, populations might have been exposed to different selective regimes, such as urban versus rural populations (Miranda et al., 2013), captive versus wild populations (Herborn et al., 2010) or different housing conditions among captive populations (Zocher et al., 2020). In addition,

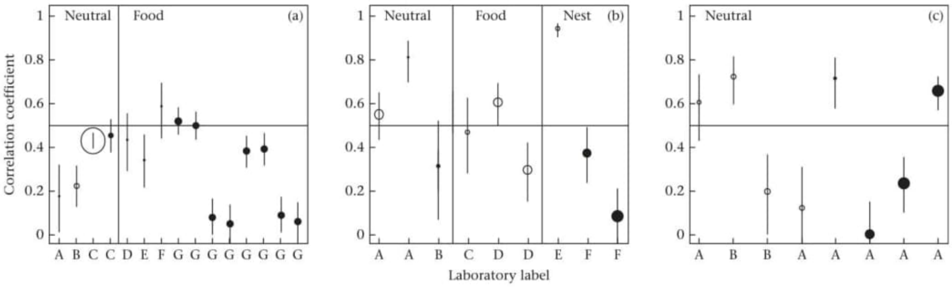

Figure 6. Repeatability (estimates ± SE) of behaviour in different testing contexts (position of novel object relative to food or the nest) for the most popular species in our data set: (a) zebra finch, *T. guttata*, (b) great tit, *P. major*, and (c) guinea pig, *C. aperea*. Open and filled dots are used to indicate short and long time intervals, respectively. The size of the dots is scaled by sample size. Different letters for the laboratory label mark different populations of animals. Horizontal lines represent zero.

population size might affect the amount of standing genetic variation and thus the phenotypic variation for behavioural traits. Moreover, the season or other environmental differences might affect the magnitude of state-dependent individual differences (Sih et al., 2015), which might arguably be larger in the wild than in captivity, although empirical evidence is scarce. Any such differences in population background, population size and the magnitude of state variation could give raise to heterogeneity in effect sizes. Hence, heterogeneity might well have a biological origin that is relevant for our understanding of variation in individual behavioural traits related to personality.

However, it is also important to consider the nonexclusive alternative, that experimental set-ups of novel object trials differ in how reliably they capture individual differences. This is an important concern, since most studies used response to novelty as a trait to be correlated with other behaviours (Guenther & Brust, 2017), endocrine measurements (Arnold et al., 2016) or reproductive success (Schielzeth et al., 2011) and these relationships might be systematically underestimated if behavioural measurements contain substantial measurement error. For example, experimental set-ups might assess different responses depending on short-term state fluctuation (e.g. in the state of hunger). Furthermore, we usually know far too little about which objects might trigger sufficient interest in animals and which objects are perceived as intimidating, which is likely to be influenced by size, colour, shape and odour of the object as well as familiarity with similar-looking objects. Objects that are perceived as scary or intimidating might trigger fear responses, while neutral objects might trigger more of an explorative response. Some of the heterogeneity in effect sizes might not represent differences in behaviour between individuals, but rather variation in novel object trials themselves, thus potentially impairing robustness of the paradigm.

Under the premise that novel object trials are designed to measure context-general personality traits, we would expect consistent findings within species or at least within populations of the same species. However, the between-species component of heterogeneity was very low and replicate studies within three specific species (guinea pig and cavies, zebra finch and great tit) show substantial differences in estimates (Fig. 6). It could be argued that these reflect genuine population differences in the case of the zebra finch and great tit, since these studies were all done mostly in different populations. This explanation seems unlikely in the case of the guinea pig, however, as all studies were performed in the same laboratory and replicated with two different populations of animals. The inconsistency across these studies is thus of potential concern.

Specific Design Decisions

Choice of novel objects is very important, as it can induce different reactions (Greggor et al., 2015). Interestingly, experimental design decision such as the use of the same or different novel objects for the test replications seems to play a very minor role in influencing the magnitude of individual differences, since on average estimates were not significantly affected. However, the vast majority of short-term repeatability estimates used different novel objects (Appendix Fig. A4). This is a useful decision for the test set-up for two reasons. First, shorter time intervals will make it more likely that individuals remember specific objects (Bell et al., 2009). Second, novel object trials are intended to quantify context-general aspects of behaviour; hence, it is the repeatable component in response to different objects that matters in most cases. Over extended time periods, however, it seems less likely that individuals would remember a specific encounter. Indeed, about half of the long-term studies used the same novel objects, with retesting done months or years after a first encounter. This design had no systematic effect on the magnitude of consistent individual differences, suggesting that the quantified behaviours are as comparable as trials with different novel objects.

The phylogenetic relationship matrix that we fitted in the meta-analytic model did not explain a significant amount of variation. However, when splitting the data by classes of animals, we found not only that mammals and birds were the most popular subjects in novel object trials, but also that they showed higher average repeatabilities. This might be due to sampling bias within groups but might also indicate that these groups are particularly suitable for testing novel object responses. It seems plausible that highly visual organisms, such as birds and many day-active mammals, are particularly suitable for novel object trials. The biased use of different groups is in agreement with the uneven representation of taxonomic classes observed by Rosenthal et al. (2017). Our view on the consistency of responses to novel objects is thus strongly dominated by these two groups of vertebrates.

Overall, we found only minor publication bias in the published record. Furthermore, we found no difference in the magnitude of repeatability estimates between studies that focus on novel object responses as the sole behaviour as compared to the large number of studies that combined multiple testing paradigms to evaluate personality dimensions. The robustly large amount of individual variation in response to novel objects reliably produces significant repeatabilities, such that there is little scope for selective reporting and thus publication bias (Forstmeier et al., 2017). Encouragingly, both the average sample size of repeatedly tested individuals and the time interval between the test repeats have increased over the years. In recent years, a typical sample was around 50–60 individuals retested after about 1–2 months. If this trend continues, it will reveal more reliable estimates and provide more data on long-term behavioural consistency.

Terminology

Besides the question of how well novel object trials allow a quantification of consistent individual differences, another important question is which personality axis they are best ascribed to: a problem of labelling and validity. Many publications in our analysis dive straight into labelling. Many published abstracts, for example, use terms like 'boldness' and 'exploration' without stating how these were quantified. However, mentioning the label is usually not conclusive enough (Kaiser & Müller, 2021). Boldness and exploration are particularly ambiguous labels, since they are also often used for startle response and open field tests, respectively. Neophilia, or even more precisely object neophilia, is a less ambiguous term that is almost exclusively used for behaviour in novel object trails. We suggest that abstracts, and not only methods sections, should clearly state the testing paradigms that were used in the quantification of individual differences.

Neophobia/neophilia might be seen as a component of exploration–avoidance. Neophobia, in particular, might also be interpreted as a behavioural response to a risky situation. It is often unclear whether an animal will perceive a novel object as risky or neutral. If this were clear, one could draw a fine line between neophobia as response to risky novelty (more in line with shyness–boldness) and neophilia as response to neutral novelty (more in line with exploration–avoidance). Réale et al. (2007) indeed grouped neophobia/neophilia with exploration–avoidance and excluded novel situations from the definition of shyness–boldness. However, our survey shows that many empirical papers (including those published after 2007) do not follow this definition, since novel object responses are often interpreted as a measure of shyness–boldness. In most cases, how animals perceive the situation will not be known and a differentiation will thus remain ambiguous.

The most frequent terms used to describe the animals' reactions to a novel object were neophobia (37 studies), neophilia (10 studies), shyness–boldness (31 studies) and exploration–avoidance (22 studies). A few studies used multiple labels. An important difference between these terms is the testing context used for their assessment. The term neophobia was mostly used when the novel object was placed in or close to a food source or close to the nest (thus amplifying the risk aspect). This seems suitable if animals are motivated to approach a food source or a nest but are prevented from approaching by 'fear of the new'. The effect is likely to be even stronger when the object is placed close to the nest than when placed close to food. When the novel object was placed in a neutral position (e.g. in the middle of the testing cage), the use of terms was distributed more evenly, which can be interpreted as novelty being seen as something to be discovered and explored (thus amplifying the exploratory aspect), or as a risky situation that induces neophobia and thus requires boldness to approach.

It may be worth studying whether novel object responses in a neutral context are better correlated with exploration and novel object responses close to food or the nest better correlated with startle responses. However, we are not aware of any systematic review on that matter. For the time being, it seems best to label responses to novel objects as object neophilia (in a neutral context for nonscary objects) and object neophobia (in a non-neutral context) and to clearly specify whether objects were placed close to a resource. The non-neutral context might be either a food source or a nest. Systematic studies across a range of taxa are needed to establish whether object neophobia/neophilia is best grouped with shyness–boldness or exploration–avoidance or kept separately as one axis neophobia–neophilia or two axes (neophobia and neophilia). We predict the best solution will depend on subtleties of the set-up in how neophobic/neophilic tendencies affect behaviour in risky and novel situations.

Over- and under-labelling in personality research gave rise to a phenomenon called the jingle–jangle fallacy (Carter et al., 2013) where there is either over-pooling (jingle) or over-separating of terms (jangle). Both cases can be found in the novel object literature. More experimental evidence is needed to disentangle or to merge behavioural terms, due to unknown underlying mechanisms. For the time being, we think it is overall better to err on the jangle side and to over-separate rather than conflate different personality axes.

Conclusions

We evaluated current practices of the novel object test and estimated average effects when novel object trials are used to assess the magnitude of temporally consistent individual differences. We found that most studies replicated novel object trials, that sample sizes have increased significantly over time and that there are more long-term than short-term assessments of behavioural consistencies. This illustrates overall good and improving research practice. Average consistencies tended to be even slightly larger than average behavioural consistencies across different testing paradigms, illustrating that the novel object paradigm is suitable for the quantification of individual differences in behaviour. Moderators in our analysis did not explain a large amount of heterogeneity. Almost all short-term studies used different novel objects for the trial repeats, which seems important, while long-term studies used either the same or different novel objects. Our results suggest that the latter decision does not affect the results. While there is some variation in how behavioural traits are labelled, the most specific description would be object neophobia/neophilia, which can be interpreted as a component of shyness–boldness or exploration–avoidance. This suggestion is based on the level of the behavioural response only and cognitive and neurophysiological studies are needed to explore the processes that lead to these behaviours. Such studies might suggest a different categorization (splitting or pooling of terms), but we think it is important to establish a clear labelling at the level of behaviour in the first place. Owing to overlap of labels with other testing paradigms, we suggest that abstracts of published papers specify the testing set-up rather than referring only to labels.

Author Contributions

H.S. and E.T.K. conceived the project. E.T. conducted data collection and analysis with the help of HS. E.T. drafted the manuscript. All authors contributed to the interpretation of results and to the revision of the manuscript.

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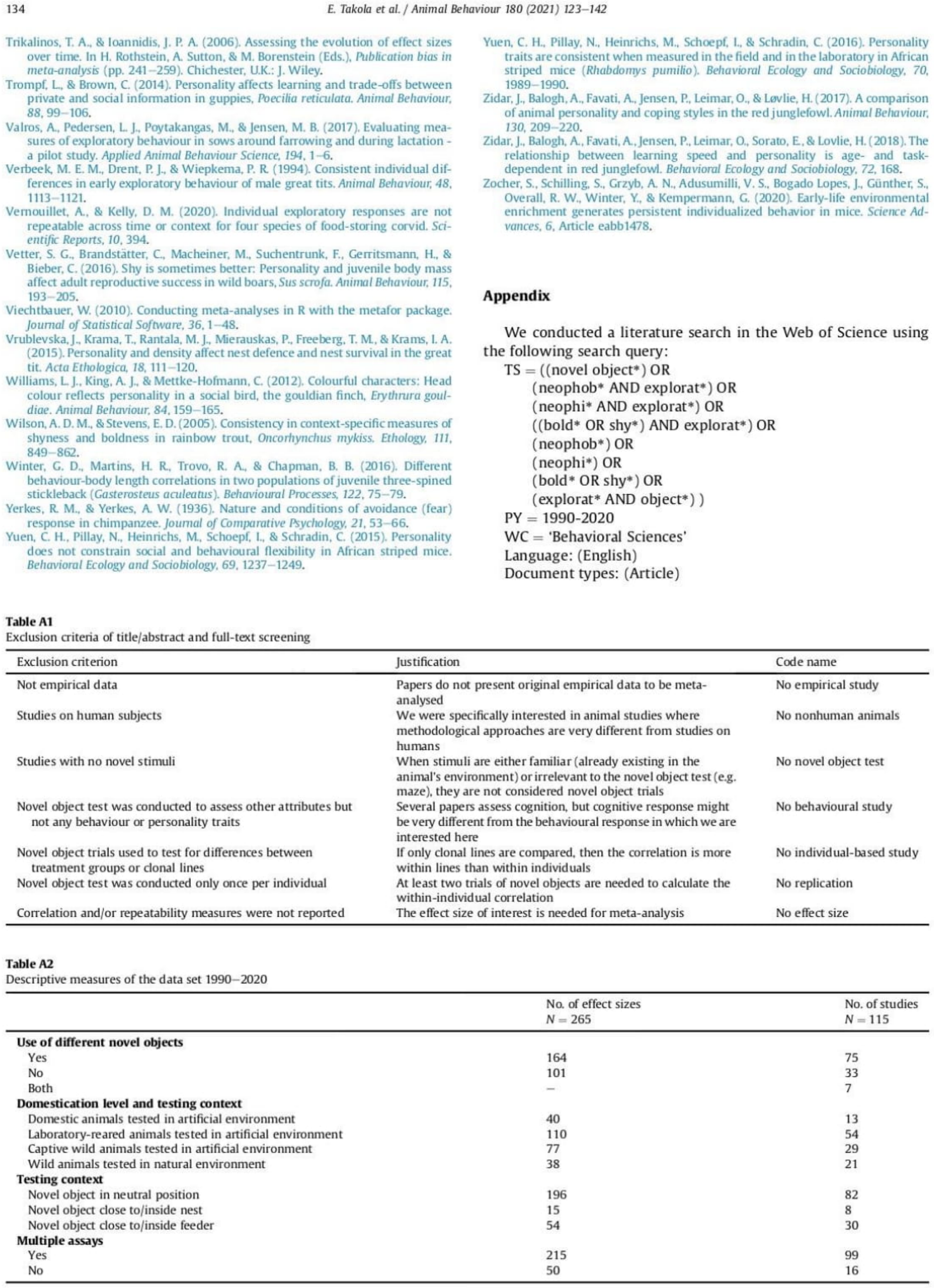

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Appendix

We conducted a literature search in the Web of Science using the following search query:

TS = ((novel object*) OR
(neophob* AND explorat*) OR
(neophi* AND explorat*) OR
((bold* OR shy*) AND explorat*) OR
(neophob*) OR
(neophi*) OR
(bold* OR shy*) OR
(explorat* AND object*))
PY = 1990-2020
WC = 'Behavioral Sciences'
Language: (English)
Document types: (Article)

Table A1
Exclusion criteria of title/abstract and full-text screening

Exclusion criterion	Justification	Code name
Not empirical data	Papers do not present original empirical data to be meta-analysed	No empirical study
Studies on human subjects	We were specifically interested in animal studies where methodological approaches are very different from studies on humans	No nonhuman animals
Studies with no novel stimuli	When stimuli are either familiar (already existing in the animal's environment) or irrelevant to the novel object test (e.g. maze), they are not considered novel object trials	No novel object test
Novel object test was conducted to assess other attributes but not any behaviour or personality traits	Several papers assess cognition, but cognitive response might be very different from the behavioural response in which we are interested here	No behavioural study
Novel object trials used to test for differences between treatment groups or clonal lines	If only clonal lines are compared, then the correlation is more within lines than within individuals	No individual-based study
Novel object test was conducted only once per individual	At least two trials of novel objects are needed to calculate the within-individual correlation	No replication
Correlation and/or repeatability measures were not reported	The effect size of interest is needed for meta-analysis	No effect size

Table A2
Descriptive measures of the data set 1990–2020

	No. of effect sizes $N = 265$	No. of studies $N = 115$
Use of different novel objects		
Yes	164	75
No	101	33
Both	–	7
Domestication level and testing context		
Domestic animals tested in artificial environment	40	13
Laboratory-reared animals tested in artificial environment	110	54
Captive wild animals tested in artificial environment	77	29
Wild animals tested in natural environment	38	21
Testing context		
Novel object in neutral position	196	82
Novel object close to/inside nest	15	8
Novel object close to/inside feeder	54	30
Multiple assays		
Yes	215	99
No	50	16

Table A3
Input variables of the meta-analytic model

Variable	Type	Code	Levels	Explanation
Study ID	Random	StudyID	Categorical: 109 studies	Unique identifier for each study
Effect Size ID	Random	EffectSizeID	Categorical: 201 effect sizes	Unique identifier for each effect size
Species	Random	Species	Categorical: 67 species	Unique species names
Sample Size	Fixed	Sample	Numerical	Number of individuals tested repeatedly
Time	Fixed	Time	Numerical	Time interval between two trials
Novelty	Fixed	Novelty	Binary: 0: no; 1: yes	Same or different objects used in repeated trials
Domestication status	Fixed	Domestication	Categorical: 1: domestic animals tested in lab; 2: lab-reared animals tested in lab; 3: wild-caught animals tested in lab; 4: wild animals tested in field	Domestication of species might affect the explorative behaviour of individuals. The place of testing might also has an impact on behavioural responses
GLMM	Fixed	GLMM	Binary: 0: no non-Gaussian linear model; 1: non-Gaussian linear model	Non-Gaussian linear models (e.g. Poisson and binomial models) often lead to lower repeatabilities
Response type	Fixed	Response	Categorical: single (behaviour); composite (of multiple behaviours); average (across multiple trials)	Composite measures and in particular averaged behaviours are expected to yield higher repeatabilities, because measurement error is reduced
Multiple assays	Fixed	MultiAssaysYN	Binary: 0: only novel object; 1: multiple behavioural tests	Whether the novel object test was the only behavioural test of the study might influence the bias towards reporting only statistically significant results
Context	Fixed	Context	Categorical: food; nest, neutral	Whether the novel object was placed next to a food item, next to or inside a nest or in a neutral spot might affect the estimate of individual differences

Table A4
Number of studies corresponding to combinations of terminology and testing contexts

Term	Neutral	Food	Nest	Total (unique)
Neophobia/Neophilia	**23**	**22**	**4**	**48**
Neophobia	13	22	3	
Neophilia	10	0	0	
Boldness–shyness	**26**	**5**	**1**	**32**
Boldness	25	5	1	
Shyness	1	0	0	
Exploration	**19**	**2**	**2**	**23**
Other terms	**10**	**0**	**2**	**12**
Activity	1	0	0	
Approach–avoidance	2	0	2	
Risk responsiveness	2	0	0	
Fearfulness	5	0	0	
No specific terms	**9**	**0**	**0**	**9**
Total (unique studies)	**82**	**30**	**9**	

Table A5
Number of studies per terminology used and moderators tested

	Neophobia/Neophilia	Boldness–shyness	Exploration
Clade			
Birds	32	7	9
Mammals	2	13	5
Fish	1	5	2
Insects	0	4	0
Reptiles	2	0	0
Context			
Food	19	4	1
Nest	3	1	1
Neutral	17	24	14
Novelty			
Different objects	32	21	10
Same object	6	9	7
Domestication status			
Domesticated	5	2	2
Laboratory-reared	10	20	5
Wild-caught (captive)	18	3	5
Wild	5	4	4

Table A6
Publications included in the final data set

Study ID	Authors (Year)	Species	Sample Size	Novel object item	Behaviour measured	Behavioural term	metaDigitize
1	Amy et al. (2017)	*Serinus canaria*	48	Red plastic round key ring, one blue oblong keyring and two gold and green metallic Eiffel towers	Latency to feed	Neophobia	No
2	An, Kriengwatana, Newman, MacDougall-Shackleton, and MacDougall-Shackleton (2011)	*Poecile atricapillus*	21	Deflated green balloon, plastic pink kazoo, fruit loops	Latency to approach	Neophobia	No
3	Arnold et al. (2016)	*Cyanistes caeruleus*	69	Pink plastic frog, half purple rubber ball	Latency to approach	Neophobia	No
4	Basic, Winberg, Schjolden, Krogdahl, and Hoglund (2012)	*Oncorhynchus mykiss*	18	Yellow rubber stopper	Latency to approach, locomotor activity, number of approaches	Behavioural response	No
5	Baxter-Gilbert, Riley, and Whiting (2019)	*Intellagama lesueurii*	83–228	Paper coffee cups, aluminium pie tins, water bottle, bag of potato chips, soft drink can	Latency to approach	Neophilia	No
6	Bibi et al. (2019)	*P. major*	24	Penlight battery, pink ball	Latency to feed	Neophobia	No
7	Boogert, Reader, and Laland (2006)	*Sturnus vulgaris*	15	Five coloured clothes-pegs, styrofoam on a cardboard plate, yellow reflective material, white opaque tube cap, white spool of light purple elastic wire, bright green opaque tube cap	Latency to feed	Object neophobia	No
8	Brust and Guenther (2017)	*C. aperea*	22	Green eggcup, yellow plastic duck	Latency to contact	Boldness	No
9	Burns (2008)	*P. reticulata*	11–36	Plastic cylinder tower with black and white stripes, purple plastic block	Latency to approach	Neophobia	No
10	Carere, Drent, Privitera, Koolhaas, and Groothuis (2005)	*P. major*	19	Penlight battery, pink rubber toy	Latency to approach	Exploration	No
11	Christensen et al. (2020)	*Equus caballus*	25	Four plastic boxes	Vigilance	Alertness	
12	Collins, Hatch, Elliott, and Jacobs (2019)	*Rissa tridactyla*	42	Ball of tissue and duct tape attached to thick wire	Latency to approach	Boldness	No
13	Coutant, Bagur, and Gilbert (2018)	*Amazona aestiva*	18–31	Plastic key toys	Behaviour scores	Neophilia	No
14	Damas-Moreira et al. (2019)	*Podarcis sicula* *Podarcis virescens*	26 29	White nonperfumed candles in foil, yellow cupcake paper, blue plastic clothes-peg	Latency to approach	Neophobia	Yes
15	Dammhahn and Almeling (2012)	*Microcebus murinus*	29–30	White wooden box with white mesh lid	Behaviour scores	Boldness	No
16	Dardenne et al. (2013)	*Hirundo rustica*	77	Christmas decorations	Latency to approach	Neophobia	No
17	David et al. (2011)	*T. guttata*	42	Small bag, soccer figurine	Latency to feed	Neophobia	No
18	DeRango et al. (2019)	*Zalophus wollebaeki*	14–33	Red, blue and yellow balls	Behaviour scores	Boldness	No
19	Devost et al. (2016)	*P. atricapillus*	78	Pink cardboard box	Latency to approach	Neophilia	No
20	Edwards et al. (2017)	*Acrocephalus sechellensis*	177	Pink toy	Behaviour scores	Exploration	No
21	Edwards et al. (2018)	*A. sechellensis*	185	Pink toy	Number of approaches	Exploration	No
22	Ensminger and Westneat (2012)	*Passer domesticus*	27	Blue ceramic vase, black, white and orange sports action figure	Latency to feed	Neophobia	No
23	Exnerova et al. (2015)	*P. major*	50	Bright blue pen, pink plastic clothes-peg	Behaviour scores	Exploration	No
24	Farrell et al. (2012)	*S. vulgaris*	40	Food dish, deflated blue balloon, corn chips	Latency to feed	Neophobia	No
25	Feenders and Bateson	*S. vulgaris*	31	Green or red light on right or left key	Latency to contact	Neophobia	No
26	Finkemeier et al. (2016)	*C. aperea*	63	Green plastic eggcup	Number of approaches	Boldness	No
27	Fox and Millam (2010)	*Nymphicus hollandicus*	45	Plastic chains, small swings, bells, mirrors, coloured wood	Behaviour scores	Behavioural response	No
28	Frost et al. (2013)	*O. mykiss*	12	Lego duplo blocks	Latency to approach	Boldness	No
29	Funghi et al. (2015)	*Estrilda astrild*	42	Green clothes-peg, pink marker	Latency to approach	Neophobia	No
30	Gabriel and Black (2010)	*Cyanocitta stelleri*	29	Feeding apparatus	Behaviour scores	Exploration	No

Table A6 (*continued*)

Study ID	Authors (Year)	Species	Sample Size	Novel object item	Behaviour measured	Behavioural term	metaDigitize
31	Garamszegi et al. (2015)	*Ficedula albicollis*	16–27	Paper sheet with small random drawings in variable colours	Latency to approach	Approach−avoidance	No
32	Garamszegi et al. (2012)	*F. albicollis*	52	White paper sheet	Latency to contact	Approach−avoidance	No
33	Grace and Anderson (2014)	*Sula granti*	86–157	Red Bull can, plastic crate	Behaviour scores	Behavioural response	Yes
34	Greenberg and Holekamp (2017)	*Crocuta crocuta*	14	Cooler, funnel, stool, bucket	Latency to contact	Neophobia & exploration	No
35	Greggor et al. (2016)	*Corvus frugilegus*	16–17	Paper and plastic customized	Latency to contact	Neophobia	No
36	Greggor et al. (2020)	*Corvus hawaiiensis*	102	Paper and plastic customized	Latency to feed	Neophobia	No
37	Grindstaff, Hunsaker, and Cox (2012)	*T. guttata*	109	AA battery, blue plastic frog	Latency to contact	Neophobia	No
38	Guenther and Brust (2017)	*C. aperea*	24	Plastic duck, Lego bricks	Latency to contact	Boldness	No
39	Guenther and Trillmich (2013)	*C. aperea*	50	Yellow plastic cup, green eggcup, red plastic pig	Latency to contact	Boldness	No
40	Guenther, Brust et al. (2014)	*C. aperea*	21	Yellow plastic cup, green eggcup	Latency to contact	Boldness	No
41	Guenther, Finkemeier et al. (2014)	*C. aperea*	62	Green eggcup, yellow plastic duck	Latency to contact	Boldness	No
42	Guenther et al. (2018)	*C. aperea*	30	Yellow plastic duck, grey plastic cylinder, green eggcup	Number of approaches	Boldness	No
43	Guido et al. (2017)	*Milvago chimango*	9	Feeding apparatus	Latency to feed	Neophobia	No
44	Gyuris et al. (2012)	*Pyrrhocoris apterus*	40	Plastic plugs	Locomotor activity	Exploration	No
45	Haage et al. (2013)	*Mustela lutreola*	68–80	Dog toys	Latency to approach	Boldness	No
46	Hebert et al. (2014)	*Betta splendens*	25	Not mentioned	Latency to feed offspring, Latency to approach, Locomotor activity	Boldness	No
47	Herborn et al. (2010)	*C. caeruleus*	43–125	Pink plastic frog, half purple rubber ball	Latency to feed, latency to approach	Neophobia	No
48	Hirata and Arimoto (2018)	*Bos taurus*	25	Plastic lanterns, frog swim ring, hand fans, elephant watering cans, plastic containers, plastic baskets, fan blades	Latency to approach	Boldness	No
49	Hopkins and Bennett (1994)	*Pan troglodytes*	49	Paintbrush, plastic cooler, dolly with three wheels, plastic board with holes, metal battery clamp, PVC configuration, metal paint roller, garage door spring, plastic pegboard, plastic seriation buckets	Latency to approach	Approach−avoidance	No
50	Jäger et al. (2017)	*Rhabdomys pumilio*	73	Plastic toys, table tennis ball	Latency to contact	Exploration	No
51	Janczak et al. (2003)	*Sus domesticus*	88	Bucket	Latency to approach, latency to contact, number of approaches, locomotor activity	Fearfulness	No
52	Johnson et al. (2015)	*Papio anubis*	43	Truck, plastic bear	latency to contact	Response to novelty	No
53	Jolles et al. (2013)	*C. frugilegus*	19	Not mentioned	Latency to approach	Boldness	No
54	Jolly et al. (2019)	*Melomys burtoni*	30	Plastic bowl	Latency to move	Boldness	No
55	Kerman et al. (2018)	*T. guttata*	30	Toys neutral colours	Latency to feed	Boldness	No
56	Krams et al. (2014)	*Ficedula hypoleuca*	40	Purple tennis ball	Latency to approach	Neophobia & exploration	No
57	Krause et al. (2017)	*T. guttata*	147	Blue AA battery	Latency to feed, number of approaches	Neophobia & exploration	No
58	Krebs et al. (2019)	*Mus domesticus*	30	Lego toy	Latency to contact, locomotor activity, latency to approach	Behavioural response	No
59	Kurvers et al. (2009)	*Branta leucopsis*	18	Green plastic mat, brown deep-pile rug	Latency to approach	Boldness	No
60	Kurvers et al. (2012)	*B. leucopsis*	44	Green plastic mat, brown deep-pile rug	Latency to approach	Boldness	No
61	Le Vin et al. (2011)	*Neolamprologus pulcher*	28	Purple plastic half sphere, red Buddha figurine	Latency to approach	Risk responsiveness	No

(*continued on next page*)

Table A6 *(continued)*

Study ID	Authors (Year)	Species	Sample Size	Novel object item	Behaviour measured	Behavioural term	metaDigitize
62	Lermite et al. (2017)	*Acridotheres tristis*	49	Green plastic hairbrush, pink doorstop	Latency to feed, latency to approach	Neophobia neophilia	No
63	Malmkvist and Hansen (2002)	*Neovison vison*	187	Wooden cube	Latency to approach	Fearfulness	No
64	Martin-Wintle et al. (2017)	*Ailuropoda melanoleuca*	18	Ice blocks, ice blocks with apple and carrot, tubs of water with two apple halves and one carrot, rubber ball	Behaviour scores	Neophobia	No
65	Mazza et al. (2019)	*Myodes glareolus*	86	Plastic toy horse, plastic toy duck	Latency to approach	Boldness	No
66	Mazza et al. (2018)	*M. glareolus*	86	Plastic toy horse, plastic toy duck	Latency to approach	Boldness	No
67	McCune et al. (2018)	*Aphelocoma californica*	16–18	Yellow plastic duck, rock	Latency to approach	Boldness	No
68	Meagher et al. (2016)	*B. taurus*	11–24	Brightly coloured ball	Latency to approach	Fearfulness	No
69	Medina-Garcia et al. (2017)	*Melopsittacus undulatus*	32	Yellow plastic cup, foraging device, small plastic statue of red dragon	Latency to contact	Neophobia	Yes
70	Meehan and Mench (2002)	*Amazona amazonica*	16	Stuffed toy chicken, miniature artificial pine tree, large plastic funnel, string of seashells, bunch of hot pink feathers, plastic action figure, red silk flower, child's sandal, screwdriver, bunch of measuring spoons, rubber duck, small woven basket	Latency to contact	Behavioural response	No
71	Mettke-Hofmann (2012)	*Erythrura gouldiae*	24	White cotton mop, brown cardboard tube with holes	Latency to feed, latency to approach	Neophobia neophilia	No
72	Mettke-Hofmann et al. (2005)	*Sylvia melanocephala* *Sylvia borin*	11 9	Cotton mop, tube with holes	Behaviour scores	Neophobia	No
73	Michelena et al. (2009)	*Ovis aries*	40	Plastic boxes with perforated lids containing different fresh herbs, coffee powder, baby's rattle, bottle brush, various baby teething rings	Locomotor activity	Exploration	No
74	Miller et al. (2005)	*Coturnix coturnix japonica*	35	Small green courgette, bright yellow plastic cup, two brown pinecones	Latency to contact	Fearfulness	No
75	Miller et al. (2006)	*C. c. japonica*	48	Small green courgette, bright yellow plastic cup, two brown pinecones	Latency to contact, latency to approach	Fearfulness	No
76	Moldoff and Westneat (2017)	*P. domesticus*	36	Blue plastic cup, clear glass jar	Latency to approach	Neophobia	No
77	Monestier et al. (2017)	*Capreolus capreolus*	21	10 geometric polystyrene shapes (circle, diamond, square, triangle) painted with contrasting colours	Number of approaches	Neophobia	No
78	Morinay et al. (2019)	*F. albicollis*	65	Coloured figurine	Latency to approach	Neophobia	No
79	Noer et al. (2016)	*N. vison*	60	Green cone-shaped dog toy, red circular dog toy	Behaviour scores	Shyness	No
80	Overington et al. (2011)	*Quiscalus lugubris*	36	Bright orange rubber ball with three nails, multicoloured ball with spikes attached to a black film canister	Latency to feed	Neophobia	No
81	Pedersen (1994)	*Vulpes vulpes*	16	Orange rubber glove mounted on a stick	Behaviour scores	Behavioural response	No
82	Perals et al. (2017)	*A. tristis*	58	Blue, green and red Lego pieces	Latency to contact	Neophobia	No
83	Pogány et al. (2018)	*T. guttata*	59	Small unpainted metal flag, small flag painted black and yellow stripes	Latency to feed	Neophobia	No
84	Rangassamy et al. (2016)	*Mus spicilegus*	37	Artificial hamburger plasticized PVC, kidney-shaped metallic box	Latency to contact	Neophobia	No
85	Rockwell et al. (2012)	*C. stelleri*	63–57	Wooden platform	Locomotor activity	Neophobia	No
86	Rohrer and Ferkin (2020)	*Microtus pennsylvanicus*	42	Oat cereal ring on a hook, glass slide smeared with white clover pulp	Latency to approach, latency to move, number of approaches, locomotor activity	Boldness Activity	No

Table A6 *(continued)*

Study ID	Authors (Year)	Species	Sample Size	Novel object item	Behaviour measured	Behavioural term	metaDigitize
87	Ruuskanen and Laaksonen (2010)	*F. hypoleuca*	57	Pink and gold toy rubber duck	Latency to approach	Neophobia	No
88	Schielzeth et al. (2010)	*T. guttata*	119–530	Dry perennial herbs, half an apple, toy ball	Behaviour scores	Neophilia	No
89	Schürch and Heg (2010)	*N. pulcher*	15–21	Model bird, beetle kitchen magnet, screwdriver, blue clamp	Latency to approach	Boldness	No
90	Siviter et al. (2017)	*Pogona vitticeps*	13	Plastic toy police van, china garden fairy, pottery wellington boot, blue plastic lamp	Latency to approach	Behavioural response	No
91	Smith and Blumstein (2012)	*Poecilia reticulata*	37	Pink soap dish, plastic baseball	Number of approaches	Exploration	No
92	Soha et al. (2019)	*Melospiza melodia*	18	Foraging grid	Latency to feed	Neophobia	No
93	Sol et al. (2012)	*A. tristis*	60	Yellow tape, green hairbrush	Latency to feed	Neophobia	No
94	Spake et al. (2012)	*S. domesticus*	567	Bucket, tennis shoe	Latency to contact	Exploration	No
95	Stöwe, Bugnyar, Heinrich et al. (2006) (A)	*Corvus corax*	6–11	Bottles, boxes, bags, cans, candles, cups	Behaviour scores, number of approaches, latency to approach	Approach-avoidance	No
96	Stöwe, Bugnyar, Loretto et al. (2006) (B)	*C. corax*	11–12	Bottles, boxes, bags, cans, candles, cups	Behaviour scores	Neophobia	No
97	Stuber et al. (2013)	*P. major*	49–61	Miniature video camera	Behaviour scores	Exploration	No
98	Tan and Tan (2019)	*Phaneroptera brevis*	48	Dog food pellet	Latency to approach	Boldness & exploration	No
99	Thodberg et al. (1999)	*S. domesticus*	26	Bucket	Latency to contact	Object exploration	
100	Tobler and Sandell (2007)	*T. guttata*	44	Iceberg lettuce, painted toy plastic dinosaurs with black eyespots	Latency to approach	Neophobia	No
101	Tremmel and Müller (2013)	*Phaedon cochleariae*	48	Red rubber plugs	Locomotor activity	Boldness	No
102	Tremmel and Müller (2014)	*Galeruca tanaceti*	51	Red rubber plugs	Locomotor activity	Boldness	No
103	Trompf and Brown (2014)	*P. reticulata*	79	Pink or yellow plastic peg, pink, blue, green or yellow pieces of Lego	Latency to approach	Boldness	No
104	Valros et al. (2017)	*Sus scrofa*	10	White plastic flowerpots, plastic cups, plastic spaghetti spoon	Latency to contact	Neophilia	No
105	Verbeek et al. (1994)	*P. major*	17–46	Penlight battery, pink panther toy	Latency to contact	Exploration	No
106	Vernouillet and Kelly (2020)	*Gymnorhinus cyanocephalus* *Nucifraga columbiana*	11 12	Red cup, green poker chip, black bottle, yellow plastic duck	Latency to approach, latency to move	Exploration	No
107	Vetter et al. (2016)	*S. scrofa*	57	Bucket, football, booster eat, toy tube, plastic basket, traffic cone, plastic crow, potato bag, watering can	Latency to contact	Exploration	No
108	Vrublevska et al. (2015)	*P. major*	21	Purple tennis ball, yellow tennis ball	Latency to feed	Neophobia	No
109	Williams et al. (2012)	*E. gouldiae*	18	Blue cork, white half cork	Latency to approach, latency to feed	Neophilia neophobia	No
110	Wilson and Stevens (2005)	*O. mykiss*	5	Feeding apparatus	latency to feed	Boldness	Yes
111	Winter et al. (2016)	*Gasterosteus aculeatus*	58	Dark plastic rain gutter	Locomotor activity	Exploration	No
112	Yuen et al. (2015)	*R. pumilio*	37	Plastic toy, white table tennis ball	Latency to contact object	Exploration	No
113	Yuen et al. (2016)	*R. pumilio*	18	Animal toy	Behaviour scores	Exploration	Yes
114	Zidar et al. (2017)	*Gallus gallus*	87–100	Spherical brown beige plush toy with large yellow and black eyes	Escape	Boldness	No
115	Zidar et al. (2018)	*G. gallus*	87	Spherical brown and beige plush toy with large yellow and black eyes	Vigilance	Neophilia	No

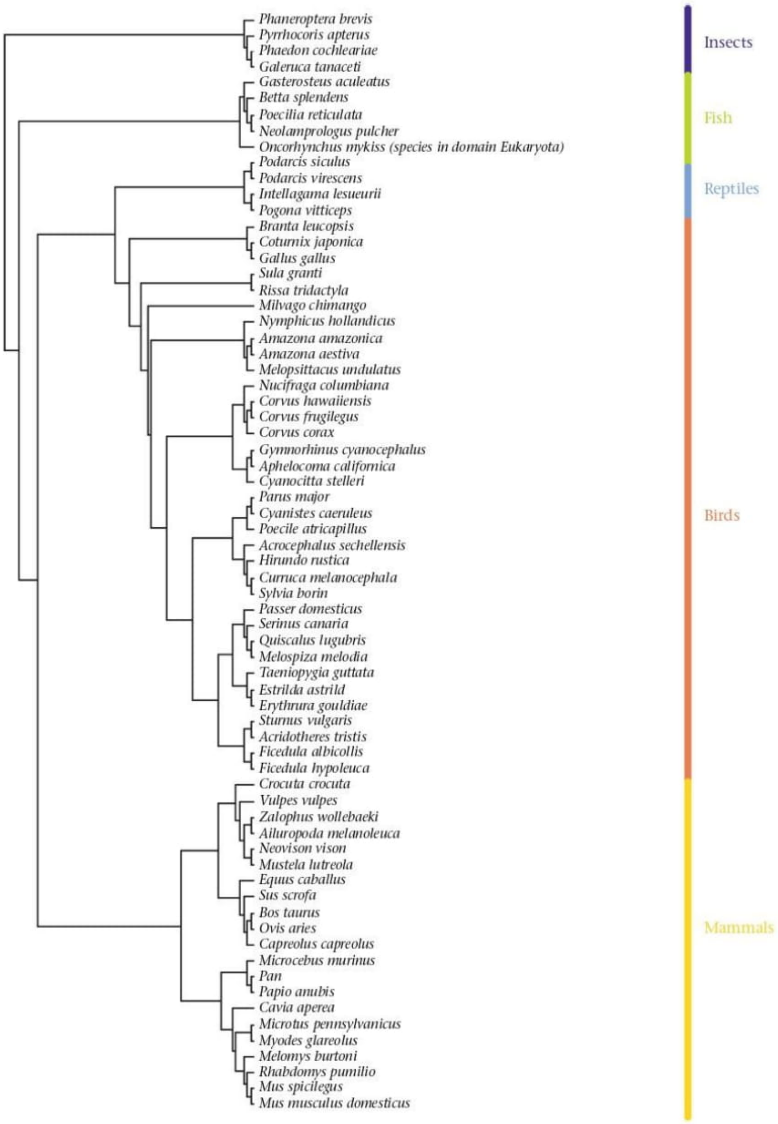


Figure A1. Phylogenetic tree of species included in the meta-analysis.

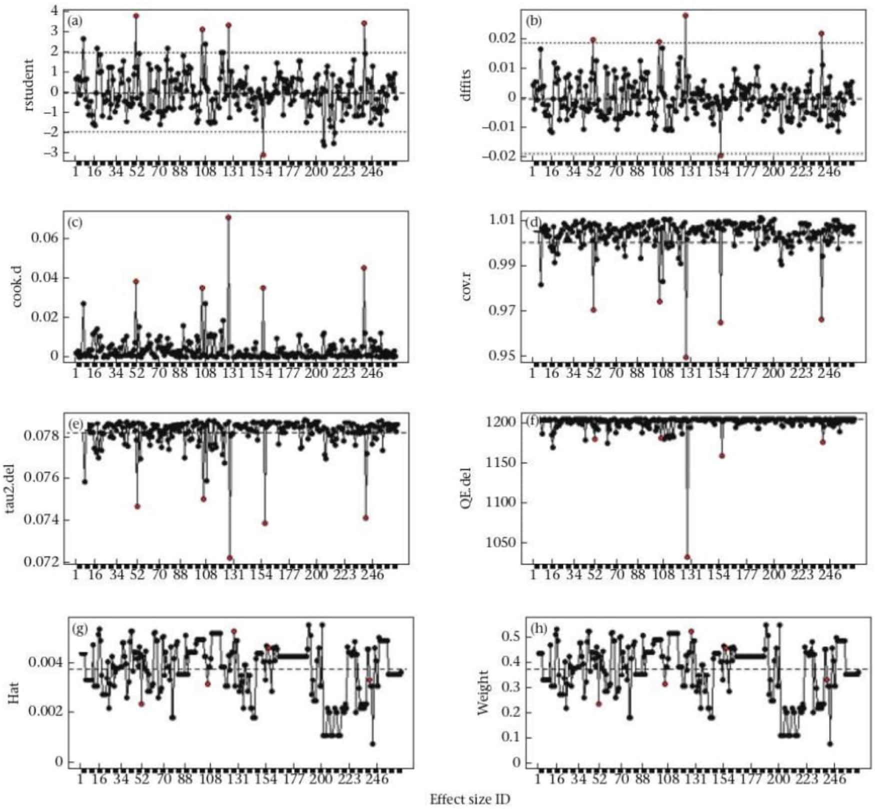
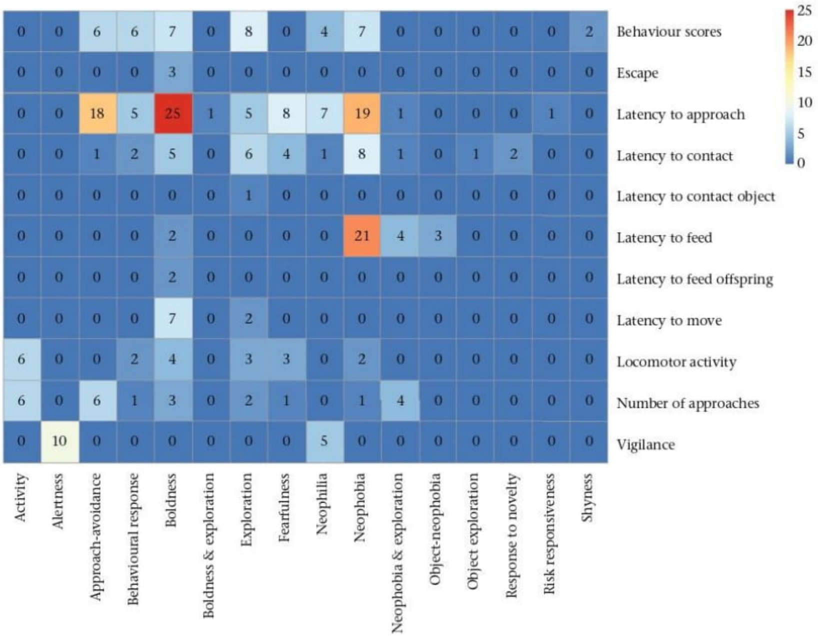


Figure A2. Influence diagnostics of effect sizes. Red points indicate outliers. *X* axes show effect size ID. *Y* axes show the scores of the following leave-one-out diagnostic tests: (a) rstudent, (b) DFFITS value, (c) Cook's distance, (d) covariance ratio, (e) the leave-one-out amount of (residual) heterogeneity, (f) the leave-one-out test statistic for the test of (residual) heterogeneity, (g) hat values, (h) weights. Dashed lines represent the overall value of each test.



	Activity	Alertness	Approach-avoidance	Behavioural response	Boldness	Boldness & exploration	Exploration	Fearfulness	Neophilia	Neophobia	Neophobia & exploration	Object-neophobia	Object exploration	Response to novelty	Risk responsiveness	Shyness
Behaviour scores	0	0	6	6	7	0	8	0	4	7	0	0	0	0	0	2
Escape	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
Latency to approach	0	0	18	5	25	1	5	8	7	19	1	0	0	0	1	0
Latency to contact	0	0	1	2	5	0	6	4	1	8	1	0	1	2	0	0
Latency to contact object	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Latency to feed	0	0	0	0	2	0	0	0	0	21	4	3	0	0	0	0
Latency to feed offspring	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Latency to move	0	0	0	0	7	0	2	0	0	0	0	0	0	0	0	0
Locomotor activity	6	0	0	2	4	0	3	3	0	2	0	0	0	0	0	0
Number of approaches	6	0	6	1	3	0	2	1	0	1	4	0	0	0	0	0
Vigilance	0	10	0	0	0	0	0	0	5	0	0	0	0	0	0	0

Figure A3. Heatmap showing the number of effect sizes by response behaviour and label for the behavioural phenotypes.

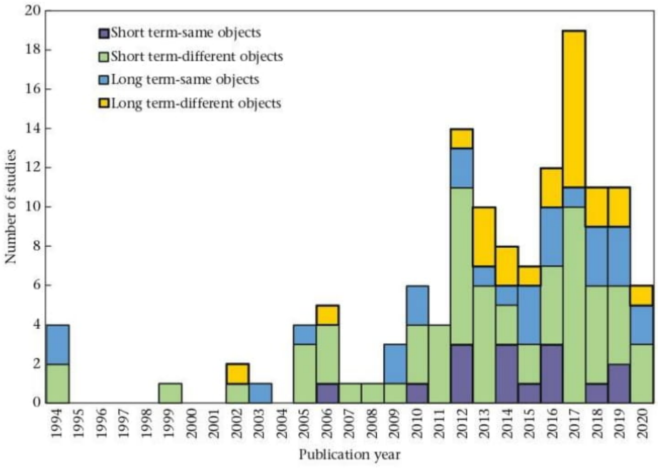


Figure A4. Number of studies per year. Different colours represent the use of same or different objects during repeated trials of the novel object test.

The little owl (Athene noctua), according to Greek mythology, represents and accompanies Athena, the goddess of wisdom. It will also accompany the following discussion, which is this thesis' attempt to produce knowledge. © Elina Takola

“…*And I think scholarship is a big tent and we should allow lots of diversity.*

I mean, essentially, scholarship is an anarchist society.

But anarchy is also subscribed to common principles and goals.”

(R. McElreath plenary talk in SORTEE 2021 conference)

General Discussion

Social changes and technological advancements during the last century revolutionized ecological research. We now have the tools to conduct research that some decades ago was unthinkable; we can track individual animals in the field via satellite, analyze big data and predict the future distribution of species. The trade-off is that scientific sub-disciplines have become very specialized. As such, publications produced by one sub-discipline might be incomprehensible to readers from another sub-field. As a result, this degree of specialization hinders the scientific discourse between relevant sub-fields. This situation is clearly visible in the case of the ecological niche; each research community has its own definition and perception of the concept. As a result, the concept of a niche is independently shaped according to the researchers' study system, research questions and academic background.

In Manuscript 1, I showed how the ecological niche concept has evolved by segregating each feature of interest and then recombining them in meaningful ways. The specific features of interest were the study species, study areas, type of study, content, temporal trends, keywords, author collaborations and co-citation patterns. I demonstrated temporal patterns of these features and discussed how the ecological niche research has changed over time. Some of the observed trends are due to the mere fact that science is growing (Seppelt et al. 2018; Réale et al. 2020), while some other results were specific to the ecological niche literature.

In Manuscript 2, I discussed some theoretical considerations regarding the concept of individualized niches. I presented a working definition, *sensu* Hutchinson (1957), before proceeding to four points of caution. Individuals exhibit consistent differences in their behaviour and no two individuals are exactly alike. As a result, their potential and realized individualized niches will differ too, due to between-individual variation. Furthermore, within-individual variation can be examined through the prism of time: the temporal changes of an organism can be treated as distinct life stages, future potential or individual life paths. In analogy to Hutchinson's definition, we considered individualized niches to be multidimensional and incorporating the intraspecific and social environment of the focal individual. Moreover, since Hutchinson's indefinite population persistence was replaced by expected lifetime reproductive success in this definition, the boundaries of the hypervolume can be both soft and hard.

Manuscript 3 constituted a study on a valuable methodological tool, which can be adopted by research on individualized niches, the repeatability of behaviour. I conducted a meta-analysis on a commonly measured behaviour, the reaction to a novel object, which is a common behavioural experiment in animal personality studies and which has plenty of ecological implications as well. The most frequent study species were zebra finches (*Taeniopygia guttata*) (also shown by Dall and Griffith 2014), guinea pigs (*Cavia aperea*) and great tits (*Parus major*). I also showed how testing practices have changed overtime, but their variation does not affect significantly the outcome, while the high overall repeatability estimate proved that the novel object test is a reliable method to study individual differences.

A new type of study, which examines behavioural differences through the lens of ecology, has emerged through mounting evidence for niche individual specialization (Araújo et al. 2011) and through methodological advances for measuring it (Bolnick et al. 2002; Ingram et al. 2018). These studies combine the methodologies from the field of animal personality with the narrative of behavioural ecology. The Collaborative Research Center NC^3 concentrates its efforts in providing evidence of individualized niches. Although the quantitative measurement of individualized niche is beyond the scope of this thesis, we aim to provide to practitioners the conceptual basis of the term, lest falling into the rabbit hole of crosstalk, tautology and jingle-jangle fallacies (Carter et al. 2013).

Traditionally, intraspecific variation is not taken into consideration in ecological studies, as it is often considered to be statistical noise (Wolf and Weissing 2012). The review by Bolnick et al. (2003) on individual niche specialization, brought to the surface an overlooked idea; that generalist populations more likely consist of specialized individuals, rather than of (ecologically equivalent) generalists (Costa et al. 2008). This variation at the level of individuals is very important not only for population dynamics, but also for inter-specific interactions (Schirmer et al. 2020; Moran et al. 2022), because individual niche variation results in fitness differences and ultimately affects ecoevo dynamics (Ponti and Sannolo 2022; Costa-Pereira et al. 2019). As a result, we observed (in Manuscript 1) a newly emerging field, which integrates behaviour into the ecological niche concept.

Meta-analysis and evidence synthesis in ecology

From a methodological standpoint, the present work comprises of an evidence synthesis project (Manuscript 1), a conceptual paper (Manuscript 2) and a meta-analysis (Manuscript 3).

Although the thesis does not include traditional data collection methods, it does provide novel insights to the ecological niche notion. I used an evidence synthesis framework, research weaving (Nakagawa et al. 2019), as a means to provide a comprehensive overview of the ecological niche literature, in order to introduce the main concept of the thesis. Manuscript 2 extended conceptual aspects of Manuscript 1, while introducing and discussing the individualized niche concept. Manuscript 3 was a meta-analysis, which focuses on evidence related to the proposed measure of individualized niches: the repeatability of behaviour. I chose the above methodologies because I believe that they serve the ultimate purpose of this thesis, which is to bring together ecological niche, behavioural ecology and animal personality.

Meta-analysis is a type of evidence synthesis. Evidence synthesis and meta-analysis appeared in ecological research quite recently (Arnqvist and Wooster 1995). Ecology is a very dynamic field; it has changed and evolved overtime (Réale et al. 2020). Meta-analysis contribute to the synthesis of results from different studies that use different methods, while accounting for these differences (Patsopoulos et al. 2008; Ioannidis et al. 2007). Evidence synthesis is the most effective toolbox to summarize literature in a comprehensive way, while meta-analyses often help to resolve scientific debates. In addition, the overproduction of data, in combination with questionable scientific practices (Fraser et al. 2018; Young et al. 2008) highlighted the need for a tidy-up in ecological literature. The scientific community was quick in its response: currently there are many initiatives that promote open science (O’Dea et al. 2021; Foster and Deardorff 2017; Haddaway et al. 2022) and address systemic issues in academia (Smaldino and McElreath 2016; Haddaway

2018; Nakagawa et al. 2020; Culina et al. 2020), while providing guidelines for ecologists (Nakagawa et al. 2017; James et al. 2016).

In conclusion, evidence synthesis is the combination of available information, in a comprehensive way. It can thus help to draw general conclusions, identify knowledge gaps and highlight weaknesses of scientific practices and academic culture. As a result, new initiatives have emerged in order to address these weaknesses and multiple institutions and journals are on board (e.g. by adopting open science policies and accepting registered reports). I believe that evidence syntheses and meta-analyses pushed the need for open science to the surface, resulting into something similar to what Thomas Kuhn (1970) described as a ‘paradigm shift’.

The animal personality toolbox for measuring individualized niches

Individual differences in behaviour are positively correlated with reproduction and survival (Moiron et al. 2020; Haave-Audet et al. 2022). Although animal personality research has been criticized for omitting the evolutionary consequences of behaviour, it has provided useful methodological tools for the study of inter-individual differences (Beekman and Jordan 2017). Manuscript 3 provided a description of some of the most used tools, but at the same time it highlighted some points of consideration for future researchers.

When planning experiments, it is important to consider the nature of the study species and select those behavioural traits which are more relevant to fitness (Dall and Griffith 2014; Ingram et al. 2018), the temporal scale in which individual differences are manifested (Layman et al. 2015) as well as the appropriate methodology (Araya-Ajoy et al. 2015; Niemelä and Dingemanse 2018; van Oers et al. 2005). The meta-analysis of Manuscript 3 showed that the sample size and the time interval between consecutive measurements have increased in the last three decades. This observation reflects an improvement of testing practices because it provides more robust estimates. In addition, I provided estimates for different classes of time interval (short and long-term repeatability) aiming to highlight that, when designing an experiment, the time intervals between measurements should be chosen carefully, to ensure that it is ecologically relevant to the study species. Previous studies which tested the impact of testing context on the relationship between behaviour and fitness proxies, found no effect (Haave-Audet et al. 2022). I extended this finding in Manuscript 3, by showing that testing context does not affect the repeatability of behaviour. These results can be the answer to robustness-related critiques of testing animals under controlled conditions.

Another challenge for researchers is to determine under which circumstances personality differences are adaptive (Dall et al. 2004; Dingemanse and Wolf 2013; Wolf and Weissing 2010; Magurran et al. 1998). But in my opinion this is a topic for another thesis.

The problem of scales

The individual as a unit

Discussions among NC^3 members highlighted a practical issue: are individualized niches really about individuals (Kaiser and Müller 2021)?

In theory, we consider each individual to be a unique combination of its genes and environment. The concept of individualized niche considers the individual as its unit, as I showed in Manuscript 2. However, in practice, it is neither informative nor realistic to treat every single individual separately in an analysis. In order for scientists to make inferences about individual niche specialization, some degree of grouping is required, at least during the stage of statistical analysis (see Manuscript 3). After contemplating a lot over issues of organismal scale, I arrived at the conclusion that when we are talking about individual niche specialization, we are rather interested in the relative differences of individuals and their frequencies, instead of what each individual is actually doing.

But what is an individual? Is a coral an individual or a colony of individuals? The discussion about what constitutes an individual has been analyzed in detail by another PhD thesis, also part of NC^3 (Trappes 2021). There are specific characteristics that help biologists distinguish among individuals (Kaiser and Trappes 2021). However, for most animal and plant species in ecological niche studies, individuals are easily distinguished, thus this discussion is beyond the scope of the present thesis.

The dimension of time

The temporal aspect of ecological niche is a very important and often overlooked point. There are multiple ways, not mutually exclusive (Hut et al. 2012), in which we can consider time. On one hand, time can be examined as a dimension of ecological niche. For example, some species are nocturnal, while some others diurnal. On the other hand, time can be considered an independent axis along which, niches change. The first case is termed ontogenetic niche shift, when the time axis refers to the lifespan of an individual and climatic niche shift, in the second case, when the time axis spreads over a much longer period (often evolutionary times).

Ontogenetic niche shifts are relevant only at the level of individuals, so in Manuscript 2 I presented different methods of structuring time (distinct life stages vs. continuous life paths). It is logical that, as individuals age, they go through developmental changes and differentiate their behaviour and interactions with their environment. Changes in behaviour can be quantitatively estimated through repeatability measures. Therefore, what I showed in Manuscript 3 is that the repeatability of behaviour declines as the time interval between measurements increase (from days to weeks to years). This means that individuals change their behaviour as they age and if we want to estimate individualized niches, we will have to choose an appropriate time scale.

Although in this thesis I do not discuss my research in terms of evolutionary scales, I believe that a synthesis of both aspects is the most reliable way to incorporate the time dimension in the ecological niche concept (Smith et al. 2019). Time is too complex a concept to be downgraded into just a one dimensional niche.

Geographical scale

Ecological niche has been historically defined in terms of impact, requirements, species-habitat relationships or trophic habits. In Manuscript 1 I showed that 'niche as a hypervolume' (i.e., where a species does or can live) is currently the predominant approach in ecological research. Why?

I think there are various reasons for this:

i) not enough systematically collected data on biotic interactions (e.g., community dynamics in the field);
ii) plenty of data on species occurrences;
iii) methodological advances (e.g., the Maxent software);
iv) inability to think in terms of systems (single species approach, although this has gradually begun to change);
v) Species distribution models are a very good playground for Ecology students;
vi) Many other questions fields got saturated (e.g. habitat selection and trophic habits).

Over the last decades, 'niche as a hypervolume' has gained ground, because one of the few rich sources of data that ecologists have at their disposal is geographical locations of presences (and less often absences) of species. This valuable source of data is usually coupled with climatic maps and other environmental layers as a means to estimate a species niche. There are many issues regarding the use of such data and numerous studies have tried to describe and resolve those issues (Feng et al. 2019; Peterson et al. 2020), but the main issue as far as my present work is concerned, the resolution of these data is usually too coarse to study intrapopulation dynamics. In addition, sampling effort is not homogeneous across locations, habitats, climatic bioregions, taxa and time (Chase and Knight 2013; Troudet et al. 2017; Meyer et al. 2015; Girardello et al. 2019; Bowler et al. 2022; Geldmann et al. 2016). These pitfalls shall be kept in mind, when collecting data for future studies.

Individuals make their way through space and time on a different scale than populations. For example, an individual can live a few years, while a population can persist for many centuries. An individual has a particular home range, whereas the distribution of populations is studied at a coarser scale. This difference in scales complicates the statistical exploration of ecological niches in an integrative way (Soberón 2007). However, a new modelling approach, called individual- or agent-based modelling, is increasingly used in ecological studies, in order to overcome the problem of scales. Individual-based models are on the rise (Aarts et al. 2008) and might provide important insights in individual niche specialization (Schirmer et al. 2019; Patterson et al. 2017; Romero-Mujalli et al. 2019).

To conclude, I think that it is essential for ecologists who intend to study individualized niches to reconsider data collection and analysis methods, while focusing on the eco-evolutionary consequences of individual differences. However, this does not mean that they ought to start from scratch and re-invent the wheel; data that has been collected at the level of individuals or populations can be re-analyzed (Pearman et al. 2008), across scales (Fig. 3), as nowadays we have the means to partition biological variation (Stoffel et al. 2021).

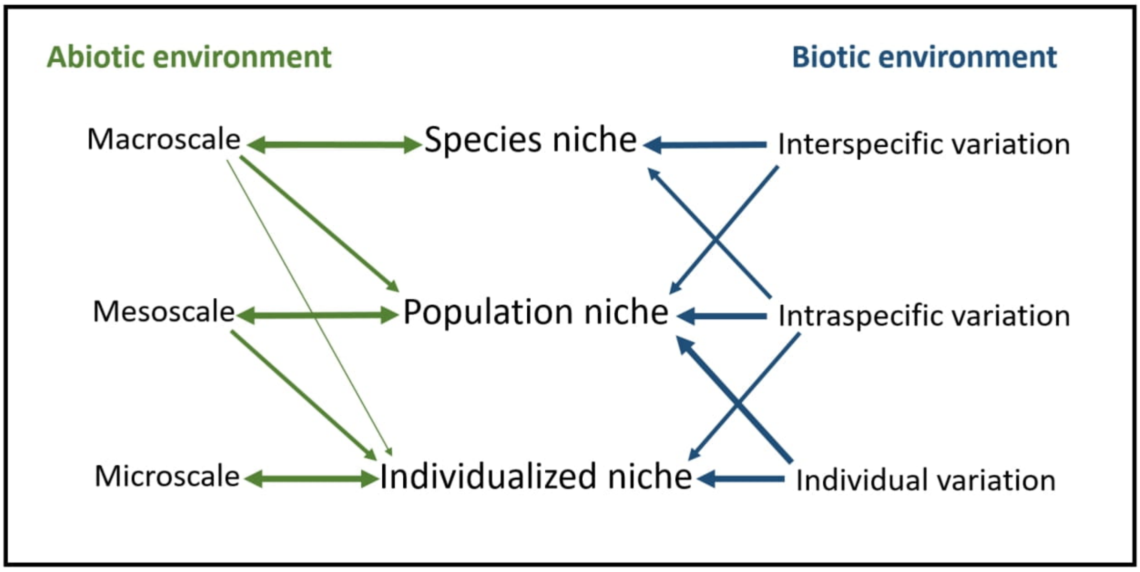


Figure 3. The relationships of environments and niches across scales. The direction and weight of arrows represent the direction and strength of effects.

The future of ecological niche

Is the niche a property of the species, as suggested by Elton, or the environment, as suggested by Grinnell (McInerny and Etienne 2012b; McInerny and Etienne 2012c)? Some studies argue that it is the former (Sillero et al. 2021; Kearney and Porter 2009), while others the latter (Alley 1982; Holt 2009b). Soberón (2007), in an landmark review on niches and distributions, suggested an integration of the three most-used approaches of the niche; data on species distributions can be distinguished in environmental variables (Grinnell's approach) and biotic interactions (Elton's approach), while Hutchinson's realized vs fundamental concepts apply to both sets of variables.

Ecological niches can be reconstructed either experimentally (Colwell and Fuentes 1975), by testing some measures of species performance under different conditions, or statistically, using individual fitness functions or species distribution models (Holt 2009b). In addition, the trade-offs behind species coexistence and the rise of meta-community ecology have provided important insights into the causes and consequences of niche differentiation (Kneitel and Chase 2004). However there is still need for a robust conceptual framework that will facilitate the interpretation of ecological niche models (Warren 2012).

Importantly, what is perceived as crosstalk by review papers' authors, might in fact be a discourse among different schools of thought (McInerny and Etienne 2012a). Conceivably, early papers that provided alternative definitions of the ecological niche, caused some differentiation, which resulted in the divergence of conceptual branches, giving birth to modern scientific communities (HilleRisLambers et al. 2012). The niche is a dynamic concept and over the years has undergone major changes (McInerny and Etienne 2012b), thus it is of great importance to perceive it as a process rather than a static condition (Martins 2017). Indeed, the high level of abstraction embedded in the concept, renders the niche (and especially the fundamental niche, see Matthiopoulos 2021) a platonic conception that is nearly impossible to measure in practice (Kingsland and Kingsland 2005). Maybe we shall move towards a more real-world-data-driven study of the niche, instead of using idealized models or highly artificial laboratory experiments (as suggested by Alley 1982).

It might be the expectation of the reader that this thesis reaches its climax with a definition for the ecological niche. I will refrain from doing so. Apparently we do not need yet another definition of the ecological niche. I agree with McInerny and Etienne (2012b) in their claim that we should adopt an abstract version of the concept when talking at a theoretical (universal) level and decide on its specific features accordingly, whenever we want to apply it in different contexts. Indeed, researchers from different backgrounds are already using specific aspects of the ecological niche as they see fit. For example, in ectotherms, it is quite common to study the 'thermal niche' (Frishkoff et al. 2015; James et al. 2006; Collin et al. 2021). Trophic niche is also a frequently studied aspect of niche, in both vertebrates and invertebrates (Crawford et al. 2008; Iken et al. 2001). The results of Manuscript 1 confirm this statement, because the major methodology to study trophic niches (stable isotope analysis) is one of the trending terms since its introduction (Boutton et al. 1983). It is thus clear that by placing an adjective in front of the word niche, it can become a pragmatic and measurable concept.

Where do we go from here? The future of individualized niches

The outcomes of NC^3 highlighted the need to join forces with scientists from other disciplines, in order to delineate the individualized niche concept. It is important to adopt a multi-disciplinary approach, by integrating social environment (Bergmüller and Taborsky 2010), physiology (Müller et al. 2020) and abiotic environment (Oswald et al. 2020).

My aim while writing this thesis was to trigger a discussion among colleagues and provide an alternative conceptual boulevard, which can lead to the development of the concept. The main purpose was to discuss the term "individualized niches" and its potential to be practically applied in ecological research. Study designs involving repeated measurements in different contexts and longitudinal studies are valuable tools for this purpose. Conceptually, I consider Hutchinson's approach to the niche as the most suitable for this quest. The integration of multiple dimensions, relevant to both the individual and the population, is essential to elucidating and crystallizing the individualized niche concept.

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Summary

The ecological niche is one of the most fundamental concepts in Ecology. It has been defined as the environmental conditions required for the persistence of a species or as the role of a species in its community or as the impact of a species on its environment. The variety of definitions assigned to the ecological niche has led to controversies about its substance and even its usefulness.

Different species occupy different places in the environment, i.e. niches. When two species are found in the same place, they have to differentiate their resource use in order to avoid competition. This phenomenon occurs not only at the species level but also at the level of individuals. Individualized niches were studied initially in terms of food consumption and later the research focus was extended to behaviour.

The aim of this thesis is to bring structure to the concept of individualized niches. After a comprehensive exploration of the ecological niche, I present some considerations related to the use of individualized niche and followingly I present a meta-analysis of a behavioural paradigm.

In Manuscript 1 I establish that ecological niche is a very diverse concept by presenting a broad conceptual map and identifying research communities within scientific literature. In addition, I provide an overview of research practices when studying ecological niche. In Manuscript 2 I present a working definition of individualized niches, based on Hutchinson's approach and then I discuss some considerations that arise from the implementation of this concept. In Manuscript 3 I present a meta-analysis of a behavioural test, the novel object paradigm, as a case study of individualized niches.

This thesis intends to bring together the ecological niche concept and aspects of behavioural ecology research, in order to bring structure to the individualized niche concept. It highlights the importance of repeated measurements of focal individuals and the need for clarity when using diverse concepts.

Zusammenfassung

Die ökologische Nische ist eines der grundlegendsten Konzepte in der Ökologie. Sie wurde definiert als die Umweltbedingungen, welche für das Fortbestehen einer Spezies erforderlich sind, oder als die Rolle einer Art in ihrer Gemeinschaft oder als die Auswirkungen einer Art auf ihre Umwelt. Die Vielfalt der Definitionen, die der ökologischen Nische zugewiesen werden, hat zu Kontroversen über ihren Inhalt und sogar ihrer Nützlichkeit geführt.

Verschiedene Arten nehmen unterschiedliche Plätze in der Umwelt ein, d. h. Nischen. Wenn zwei Arten am gleichen Ort vorkommen, müssen sie ihre Ressourcen unterschiedlich nutzen, um Konkurrenz zu vermeiden. Dieses Phänomen tritt nicht nur auf der Ebene der Arten, sondern auch auf der Stufe der Individuen auf. Individualisierte Nischen wurden ursprünglich im Hinblick auf den Nahrungsverbrauch untersucht und später auf das Verhalten ausgeweitet.

Ziel dieser Arbeit ist es, dem Konzept der individualisierten Nischen Struktur zu verleihen. Nach einer umfassenden Untersuchung der ökologischen Nische stelle ich einige Überlegungen zur Verwendung der individualisierten Nische an und präsentiere anschließend eine Meta-Analyse eines Verhaltensparadigmas.

In Manuskript 1 stelle ich fest, dass die ökologische Nische ein sehr vielfältiges Konzept ist, indem eine umfassende konzeptionelle Karte vorgestellt wird und Forschungsgemeinschaften in der wissenschaftlichen Literatur identifiziert werden (in my opinion the passive sounds better). Zusätzlich gebe ich einen Überblick über die Forschungspraktiken bei der Untersuchung ökologischer Nischen. In Manuskript 2 stelle ich eine Arbeitsdefinition von individualisierten Nischen vor, die auf dem Ansatz von Hutchinson beruht, und erörtere anschließend einige Überlegungen, die sich aus der Umsetzung dieses Konzepts ergeben. In Manuskript 3 präsentiere ich eine Meta-Analyse eines Verhaltenstests, des Novel-Object (neuartiges Objekt) Paradigmas, als eine Fallstudie über individualisierte Nischen.

Diese Arbeit ist ein Versuch, das ökologische Nischenkonzept mit Aspekten der verhaltensökologischen Forschung zu verbinden, um dem Konzept der individualisierten Nische

Struktur zu verleihen. Sie unterstreicht die Bedeutung von wiederholten Messungen an den im Fokus stehenden Individuen und die Notwendigkeit von Klarheit bei der Verwendung verschiedener Konzepte.

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Half of the time of this PhD, we had to live through the COVID19 pandemic. This situation took a mental health toll on all of us. Special thanks to all the fellow lab members and my friends for helping me to cope on a daily basis. This journey will now be continued with lots of good memories.

Eigenständigkeitserklärung

Declaration of independent assignment

I hereby confirm that I am familiar with the valid doctoral examination regulations, I produced the doctoral thesis project myself, I have not used any text passages from third parties nor their own previous final theses without citing those and I have cited the tools, personal communication, and sources having been used. In addition, I did not receive any assistance from specialized consultants and that any third party did not receive either direct or indirect financial benefits from the applicants for work connected to the doctoral thesis submitted. I have not already submitted the doctoral thesis project as my final thesis for a state examination or other scientific examination and I have not submitted the same, a substantially similar, or another scientific paper to any other institution of higher education or to any other faculty as a doctoral thesis.

PUBLICATIONS LIST

Published manuscripts included in the thesis

Takola, E., Krause, E., Müller, C., & Schielzeth, H. (2021). Novelty at second glance: a critical appraisal of the novel object paradigm based on meta-analysis. *Animal Behaviour*, *180*, 123-142. https://doi.org/10.1016/j.anbehav.2021.07.018

Takola, E., Schielzeth, H. (2022). Hutchinson's ecological niche for individuals. *Biology & Philosophy*, 37, 25. https://doi.org/10.1007/s10539-022-09849-y

Published manuscripts not included in the thesis

Moran, N., Caspers, B., Chakarov, N., Ernst, U., Fricke, C., Kurtz, J., Lilie, N., Ka Lo, L., Müller, C., R, R., **Takola, E.**, Trimmer, P., van Benthem, K., Winternitz, J. & Wittmann, M. (2021). Shifts between cooperation and antagonism driven by individual variation: a systematic synthesis review. *Oikos*. https://doi.org/10.1111/oik.08201

Trappes, R., Nematipour, B., Kaiser, M. I., Krohs, U., Van Benthem, K. J., Ernst, U. R., Gadau, J., Korsten, P., Kurtz, J., Schielzeth, H., Schmoll, T., & **Takola, E.** (2022). How Individualized Niches Arise: Defining Mechanisms of Niche Construction, Niche Choice, and Niche Conformance. *BioScience*, 72(6), 538-548. https://doi.org/10.1093/biosci/biac023

Manuscripts in preparation

Takola, E. & Schielzeth, H. (2022). Development of the ecological niche concept. [Manuscript in preparation].

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Takola, E., Bracic, M., Hoffman, J., Mutwill, A., Nagel, R., Oswald, P. & Rystrom, T. (2022). Ontogenetic changes of between- and within-individual variation. [Manuscript in preparation]. (co-authors in alphabetical order)

Supplement

Supplement of Manuscript 1

Table S1. Frequency of each taxonomic level identified by the GNfinder algorithm.

Taxonomic level	Count
Species	4860
Genus	1198
Family	561
Order	321
Phylum	147
Class	86
Subfamily	59
Ichnogenus	20
Taxon	19
Tribe	19
Infraorder	11
Subphylum	11
Superfamily	11
Clade	10
Subclass	10
Domain	9
Suborder	6
Superorder	5
Infraclass	4
Section	4
Subtribe	4
Division	3
Subdivision	3
Superclass	3
Subgenus	2
Superphylum	2
Ichnotaxon	1
Subkingdom	1

Table S2. Frequency of document types in the complete dataset (N = 32,833 papers) per subset.

Subsets/Types of documents	Number of publications	Percentage
1930-1960		
Journal article	18	85.7%
Book/Book chapter	0	0%
Conference paper	0	0%
Other	3	14.3%
1960-1970		
Journal article	47	97.9%
Book/Book chapter	0	0%
Conference paper	1	2.1%
Other	0	0%
1970-1980		
Journal article	237	95.6%
Book/Book chapter	0	0%
Conference paper	2	0.8%
Other	9	3.6%
1980-1990		
Journal article	584	96.1%
Book/Book chapter	0	0.0%
Conference paper	5	0.8%
Other	18	3.0%
1990-2000		
Journal article	1621	91.5%
Book/Book chapter	4	0.2%
Conference paper	12	0.7%
Other	135	7.6%
2000-2010		
Journal article	4723	85.4%
Book/Book chapter	106	1.9%
Conference paper	117	2.1%
Other	583	10.5%
2010-2020		
Journal article	21696	98.8%
Book/Book chapter	455	2.1%
Conference paper	129	0.6%
Other	1474	6.7%

Table S3. Frequency of type of study for 50% (16,400 papers) of the dataset.

Type of study	Number of articles	Percentage
Primary data-Observational	7462	45.5%
Primary data-Experimental	2767	16.9%
Database	2537	15.5%
Review (narrative review or evidence synthesis)	2111	12.9%
Simulation	968	5.9%
Ideas-Concepts	332	2%
Meta-analysis	90	0.5%
Methods	67	0.4%
Software	38	0.2%
Theoretical	34	0.2%

Table S4. Country collaboration network indices for each subset.

Country collaboration network indices	1930-1990	1990-2000	2000-2005	2005-2010	2010-2015	2015-2020
Size	45	74	76	101	129	154
Density	0.002	0.032	0.09	0.105	0.128	0.211
Transitivity	Na	0.269	0.38	0.403	0.486	0.566
Diameter	1	5	4	5	4	4
Degree Centralization	0.021	0.269	0.484	0.545	0.521	0.619
Average Path Length	1	2.501	2.187	2.096	2.064	1.836

Table S5. Frequency plots for study locations referring to continents (left) and oceans (right) per year.

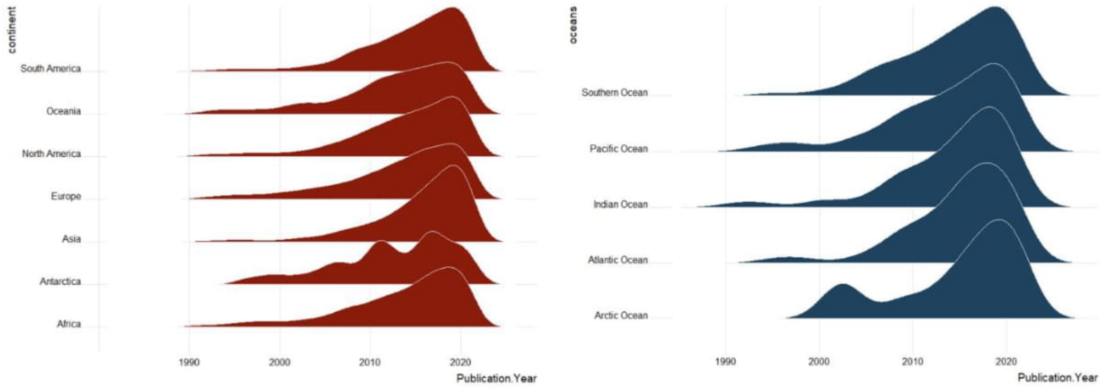


Table S6. Frequency barplot for study locations referring to seas.

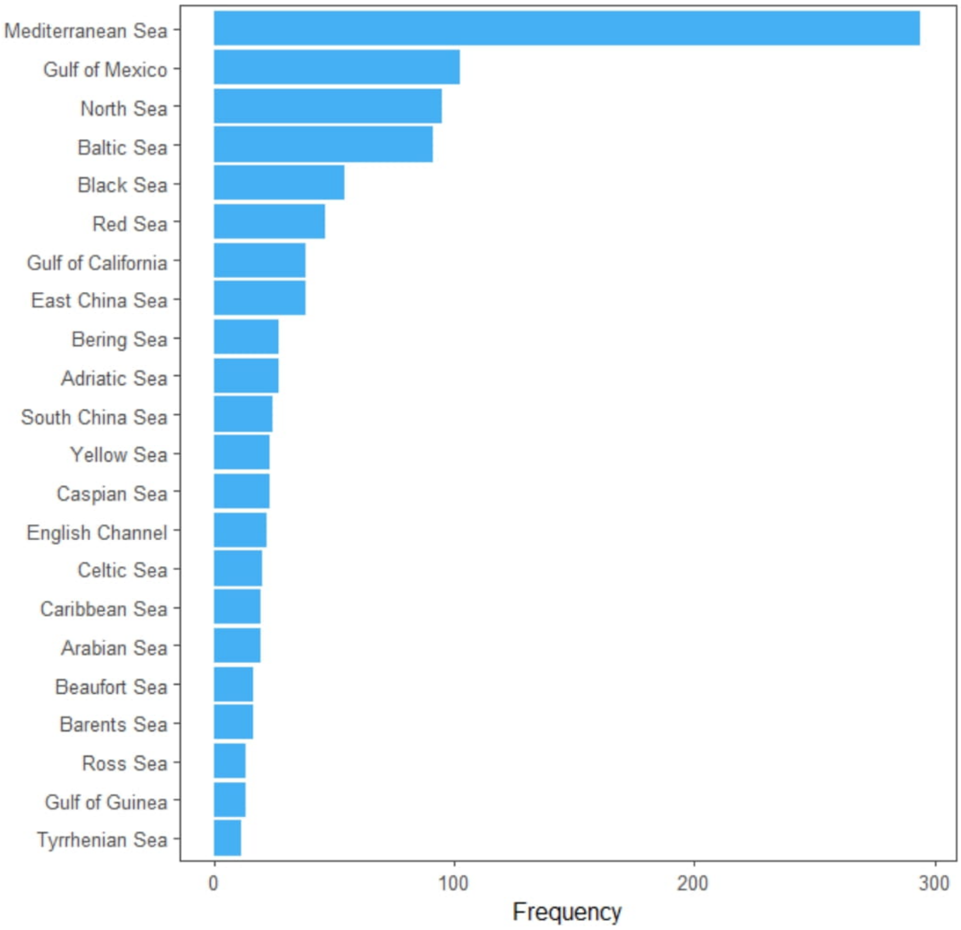


Table S7. List of hyper-topics per subset, along with the topics comprising them.

	1930-1990	1990-2000	2000-2005	2005-2010	2010-2015	2015-2020
CHINESE ECOLOGY	NA	NA	NA	NA	83	73
CLIMATE CHANGE	NA	NA	40	9	102	36
INVASION ECOLOGY	NA	38	11	6	109	65
ADAPTATION	NA	33	34	35,37	29,43,99	22,24,29
EVOLUTION	1,31,40	19,26,52	13,19,37,9,18,25,27	24,40,47	3,15,21,38,66,86,90,107,7,63	2,31,33,40,50,76,79,80
SOIL ECOLOGY	2,7,13	4,16,29,58	2,20,53,55,58,37	3,28,57	4,39,58,68,79,92,103	12,13,23,49,61,19
HABITAT/REPRODUCTION/ORNITHOLOGY	4,23,32	2,17,48	21,50,68	14,39,42,46,21	19,25,50,70,78,64	28,32,38,77,51
COMMUNITY ECOLOGY	5	24,30,42	24	16,20	33,94	30
URBAN/HUMAN	NA	8	3,22	18	88,92	20,26,66,70
SYSTEMS	6,29,37	7	46,65,29	38,44,25,41	51,62,81	10,25,59,68
AQUATIC/ISLAND BIOG	12,27	9,10,11,49,50,15,40	15,17,32,38,69,63,59,7,8,15,26,35,45	1,54,60,33,34,58	5,20,24,101,52,110,75,11,72,87,93,47	34,45,48,60,45,71,47,12,55,44,69
FOOD	15,20,37,39	1,5,6,56,60	41,44,52,61,66	4,12,14,17,22,32,56	1,6,8,9,10,13,18,73,76,91,100,108	4,15,39,41
HOST/PARASITE	16	20	48,54	53	16,61,88,105	8,37
PLANT	17	22,28,35,36,41,46,47	51,56,57,60	8,11,52,55	12,14,44,48,60,74	17,21,43
INTERSPECIFIC	19	53	12,64	5,17	37,57,18,45,76	9,56
SEED/GROWTH	21	54,56	1,23	19	40,95	58
BEHAVIOUR	24	12,32,52,31	1,5,6,49,43	30,36,51	2,30,35,69,98	5,38,64
EXTINCTION	34	12	59	3,31	34	50

MACROECOLOGY	36	34,44,45,47	14,16,47,67	12,45,50	28,64,65,85,96,104,106	26,35,46,54,72
STRESS/TEMPERATURE/LIGHT	36	27,58	28,36,31	19,60	26,32,80,82	7,14,53
SDM	38	43,59	4,5,39,62	7,10,15,23,26,29,43,48,49	22,23,42,49,54,55,56,59,67,71,77,89	1,6,16,18,27,42,57,62,63,67,78
INSECT ECOLOGY	NA	13,23,46	30,42	6,42	19,31,61	8
CHEMICAL ECOLOGY	NA	21	70	28	NA	NA
FOREST/FUNGI	NA	25	55	59	53	13

Table S8. Descriptive measures of author collaboration for the complete dataset (N = 32,833 papers).

AUTHOR COLLABORATION	1930-1960	1960-1970	1970-1980	1980-990	1990-2000	2000-2010	2010-2020
Single-authored documents	19	34	161	322	621	925	1406
Documents per Author	0.955	0.828	0.754	0.67	0.589	0.423	0.416
Authors per Document	1.05	1.21	1.33	1.49	1.7	2.37	2.41
Co-Authors per Documents	1.1	1.33	1.5	1.72	2.22	3.33	4.81
Collaboration Index	2	1.93	2.08	2.14	2.15	2.67	2.5

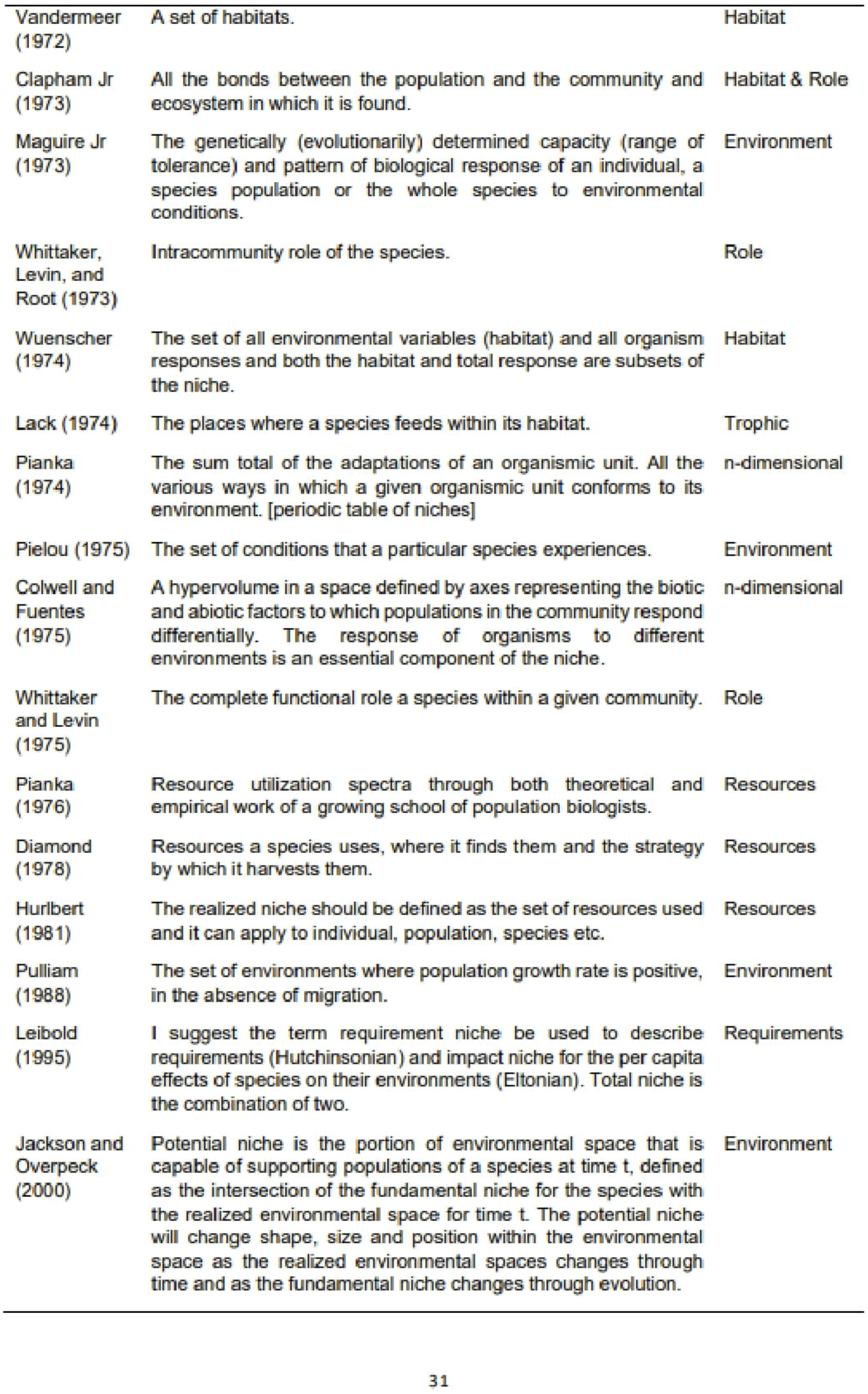
Table S9. Author collaboration network indices for each subset.

AUTHOR COLLABORATION NETWORK INDICES	1930-1990	1990-2000	2000-2005	2005-2010	2010-2015	2015-2020
Size	1056	2962	4084	9900	21101	40636
Density	0.001	0.001	0.001	0.001	0	0
Transitivity	0.866	0.865	0.934	0.751	0.658	0.522
Diameter	4	5	8	25	19	18
Degree Centralization	0.007	0.007	0.013	0.014	0.007	0.013
Average Path Length	1.211	1.53	2.509	8.332	6.649	5.589

Supplement of Manuscript 2

Table S1. List of definitions of the ecological niche (in chronological order) and their thematic category.

Reference	**Definition(quote)**	**Category**
Grinnell (1917)	Variables associated with the presence of a species (e.g. *Toxostoma redivivum*). (not quote)	Habitat
Elton (1927)	The status of an animal in its community, its place in the biotic environment, its relations to food and enemies.	Role
Grinnell (1928)	The ultimate distributional unit within which each species is held by its structural and instinctive limitations.	Habitat
Gause (1934)	Place a given species occupies in a community.	Environment
Elton (1950)	The mode of life and especially the mode of feeding of an animal.	Trophic
Dice (1952)	The ecologic position that a species occupies in a particular ecosystem, a consideration of the habitat that the species concerned occupied for shelter, for breeding sites and for other activities, the food that it eats and all the other features of the ecosystem that it utilizes. The term does not include, except indirectly, any consideration of the functions that the species serves in the community.	Environment
Clarke (1954)	The function of the species in the community, rather than its physical place in the habitat.	Habitat
Macfadyen (1957)	Niche as a multidimensional entity.[not well developed]	n-dimensional
Hutchinson (1957)	An n-dimensional hypervolume defined on axes representing all of the ecological factors relative to the species and every point in which corresponds to a state of the environment which permits the species to exist indefinitely.	n-dimensional
Odum (1959)	The position or status of an organism within its community and ecosystem resulting from the organism's structural adaptations, physiological responses, and specific behavior (inherited and/or learned).	Role
Weatherley (1963)	The nutritional role of the animal in its ecosystem, that is, its relations to all the foods available to it.	Trophic
Root (1967)	The niche is composed of several dimensions, each corresponding to some requisite for a species.	n-dimensional
MacArthur (1968)	Niche breadth is the "distance through" a niche along some particular line in niche space. (not quote)	n-dimensional
Odum and Barrett (1971)	The physical space and the functional role of a species in the community and its position in environmental gradients of temperature, moisture, pH, soil and other conditions of existence.	Habitat & Role
Van Valen (1971)	An adaptive zone in the niche of any taxon, especially a supra-specific one, and has two more or less independent components. One involves use of resources and the other involves resistance to predation and parasitism.	Resources



Vandermeer (1972)	A set of habitats.	Habitat
Clapham Jr (1973)	All the bonds between the population and the community and ecosystem in which it is found.	Habitat & Role
Maguire Jr (1973)	The genetically (evolutionarily) determined capacity (range of tolerance) and pattern of biological response of an individual, a species population or the whole species to environmental conditions.	Environment
Whittaker, Levin, and Root (1973)	Intracommunity role of the species.	Role
Wuenscher (1974)	The set of all environmental variables (habitat) and all organism responses and both the habitat and total response are subsets of the niche.	Habitat
Lack (1974)	The places where a species feeds within its habitat.	Trophic
Pianka (1974)	The sum total of the adaptations of an organismic unit. All the various ways in which a given organismic unit conforms to its environment. [periodic table of niches]	n-dimensional
Pielou (1975)	The set of conditions that a particular species experiences.	Environment
Colwell and Fuentes (1975)	A hypervolume in a space defined by axes representing the biotic and abiotic factors to which populations in the community respond differentially. The response of organisms to different environments is an essential component of the niche.	n-dimensional
Whittaker and Levin (1975)	The complete functional role a species within a given community.	Role
Pianka (1976)	Resource utilization spectra through both theoretical and empirical work of a growing school of population biologists.	Resources
Diamond (1978)	Resources a species uses, where it finds them and the strategy by which it harvests them.	Resources
Hurlbert (1981)	The realized niche should be defined as the set of resources used and it can apply to individual, population, species etc.	Resources
Pulliam (1988)	The set of environments where population growth rate is positive, in the absence of migration.	Environment
Leibold (1995)	I suggest the term requirement niche be used to describe requirements (Hutchinsonian) and impact niche for the per capita effects of species on their environments (Eltonian). Total niche is the combination of two.	Requirements
Jackson and Overpeck (2000)	Potential niche is the portion of environmental space that is capable of supporting populations of a species at time t, defined as the intersection of the fundamental niche for the species with the realized environmental space for time t. The potential niche will change shape, size and position within the environmental space as the realized environmental spaces changes through time and as the fundamental niche changes through evolution.	Environment

Pulliam (2000)	The landscape in the NICHE model (that we suggest) consists of a two-dimensional array of grid cells. The landscape represents the environmental conditions in 'ordinary physical space' and corresponds to what Hutchinson called 'biotope'.	Environment
Chase and Leibold (2003)	A joint specification of environmental conditions or variables that allow a species to have positive intrinsic growth rate along with the effects of that species on those environmental variables.	Environment
Kearney (2006)	A subset of those environmental conditions which affect a particular organism, where the average absolute fitness of individuals in a population is greater than or equal to one.	Environment
Cain, Bowman, and Hacker (2008)	The physical and biological conditions that the species needs to grow, survive and reproduce.	Environment
McInerny and Etienne (2012)	A term to describe abstractions of an organism's relationship to an 'ecosystem' as described by both effect and response interactions the organism has, both directly and indirectly, with and on other biotic/abiotic objects that are part of that ecosystem.	Environment

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Appendix

Eleni Elda Takola has produced all figures presented in Manuscript 1.

Eleni Elda Takola and Holger Schielzeth have jointly produced all conceptual figures of Manuscript 2.

Eleni Elda Takola has produced all figures of Manuscript 3. Holger Schielzeth assisted the production of Figures 2,3 and 6 of Manuscript 3.

Jena, ……………………………..

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Supervisor

“*Antarctica will be discovered only if one sails south*”

(Gosling & John 1999)