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Review

Powerful yet challenging: mechanistic niche models for predicting invasive species potential distribution under climate change

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Risk assessments of invasive species present one of the most challenging applications of species distribution models (SDMs) due to the fundamental issues of distributional disequilibrium, niche changes, and truncation. Invasive species often occupy only a fraction of their potential environmental and geographic ranges, as their spatiotemporal dynamics are shaped by intraspecific variability, human-mediated introductions, novel biotic interactions, climate change, rapid selection, and ecological niche shifts. Traditional correlative SDMs struggle to capture these processes because they implicitly assume distributions are at equilibrium and rely on observed occurrences that seldom represent the full environmental niche of invasive species. Predicting future potential distributions therefore requires moving beyond simple climate-matching approaches to models that explicitly capture the mechanisms underlying species responses to their environment. Mechanistic niche models (MNMs) are process-explicit models that address these limitations by capturing species' performance across environmental gradients. By incorporating physiological constraints and vital rates, MNMs offer a mechanistic understanding of species-environment relationships and enable more robust predictions onto novel environments. However, a unified MNM framework remains elusive. In this review, we delve into the theoretical foundations of MNMs, emphasizing their advantages over correlative approaches, focusing on invasive species. We provide insights into diverse modelling techniques across taxa and examine the benefits and limitations of MNMs for predicting species distributions under novel conditions. Our systematic review reveals that MNMs have been applied sparingly to invasive species, focusing primarily on insects and plants, likely due to high data requirements. MNMs constitute the most suitable approach for defining species distribution limits under novel conditions, but their success depends on the relevance of input data and effective parameterisation, including genotype selection, model type, experimental conditions and physiological curve-fitting techniques. MNMs offer

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significant potential for advancing ecological research and providing robust tools for evidence-based management decisions for populations in disequilibrium under changing environmental conditions.

Keywords: alien species, biophysical modelling, ecophysiological niche models, invasion risk forecasting, invaded range, metabolic rates, systematic review, vital rates

Challenges for modelling invasive species using species occurrence data

Understanding the constraints of species distribution and abundance has been a central goal in ecology for decades (Andrewartha and Birch 1954), and remains highly relevant as climate change reshapes species distributions (Sutherland et al. 2013, Pecl et al. 2017, Lenoir et al. 2020). Invasive species provide unique insights into how organisms expand their ranges and respond to novel conditions, offering a basis to understand and predict the impacts of climate change on native species distributions (Cadotte et al. 2021).

Correlative species distribution models (SDMs) are the most widely used tools for spatially explicit predictions of species' environmental suitability (Peterson et al. 2011, Guisan et al. 2017) and have been extensively applied to explore invasive species' potential (Petitpierre et al. 2012, Guisan et al. 2014). SDMs use statistical models to describe relationships between species occurrence or abundance records and spatial predictors (e.g. temperature, precipitation). These relationships are then used to map occurrence probabilities and make forecasts across time and space (Elith and Leathwick 2009, Elith 2017).

However, correlative SDMs face critical limitations (Lee-Yaw et al. 2022), including difficulty accounting for observation bias and location errors (Graham et al. 2008, Barve et al. 2011, Fernandes et al. 2018, Zizka et al. 2019), complex population dynamics (e.g. source–sink), non-equilibrium situations (Pagel et al. 2020, Scherrer et al. 2020, Sandel et al. 2025), environmental niche truncation (Bush et al. 2018, Chevalier et al. 2021a, Pang et al. 2022), and species dispersal (Engler and Guisan 2009, Václavík and Meentemeyer 2009, Wisz et al. 2013). Biased observations of species' occurrences are a challenge for all SDMs (Dubos et al. 2022), but might be even more complex for species with dynamically expanding ranges like invasive species (Václavík and Meentemeyer 2009, Gallien et al. 2012, Moudrý et al. 2024). Mitigating observational bias for alien species in their invaded ranges while addressing niche truncation (i.e. only part of the entire species' niche being captured in the model) and the impact of enemy release is more complex, as additional mechanisms beyond heterogeneous sampling effort or imperfect detection are involved, which will be discussed in detail in the following sections (Figure 1, Box 1). As a result, invasive species distributions are frequently under- or over-predicted, as current records fail to reflect their potential ranges (Hui 2023).

Given the need to understand invasive species potential distributions for global biodiversity conservation, and the limitations of correlative approaches, alternative, more mechanistic methods have been proposed (Kearney and Porter 2009, Evans et al. 2015). Among those more process-explicit models, mechanistic niche models (MNMs) incorporate physiological constraints and vital rates in response to the environment, and thus they have been proposed as a key modelling approach to understand species potential distribution to novel climates (Briscoe et al. 2019). In this review, we aim to 1) decompose the mechanisms behind the biases and limitations that cause correlative SDMs of invasive species to fail (source–sink dynamics, niche shifts, temporal dynamics, hybridisation and niche truncation), and 2) justify and define the foundations of MNMs and their potential for invasive species. While discussing mechanistic niche models, we will also 3) explore how MNMs have been applied to project invasive species' potential distributions and 4) assess when MNMs are most likely to address the limitations of correlative SDMs for invasive species.

Complex source–sink dynamics: global trade and disturbance might drive invasive species presence

The presence of species outside their native ranges is primarily a consequence of human movement across the globe (Turbelin et al. 2017). Colonisation, and more recently globalisation, has facilitated the crossing of previously impenetrable geographic barriers, sometimes even transporting species to regions (i.e. geographic space) with climatic conditions that are outside the species' native environmental niche (Lenzner et al. 2022). Transportation networks, trade and international travel now serve as effective vectors for introducing non-native species (Westphal et al. 2008, Gippet and Bertelsmeier 2021, Hulme et al. 2021).

In addition to global trade, increased propagule pressure and anthropogenic impacts might enable urbanised areas to temporally sustain invaders (Pfadenhauer et al. 2024), where urbanisation is a major driver of exotic species richness (Heringer et al. 2022). Highly populated areas experience greater invasive propagule pressure due to connectivity and global trade (Robinet et al. 2009), amplifying invasions (Son et al. 2024) and increasing the likelihood of successful establishment (Borden and Flory 2021). In addition, disturbed communities often host lower biodiversity and have been described as less resistant to invasions (González-Moreno et al. 2015), although this relationship may vary with the invasion stage (Stachowicz and Tilman 2005, Guo et al. 2024).

Accessibility to suitable habitats not only enhances range expansion but also the likelihood of species detection. Spatial autocorrelation in species records (not only in the invaded range) often reflects uneven sampling efforts and

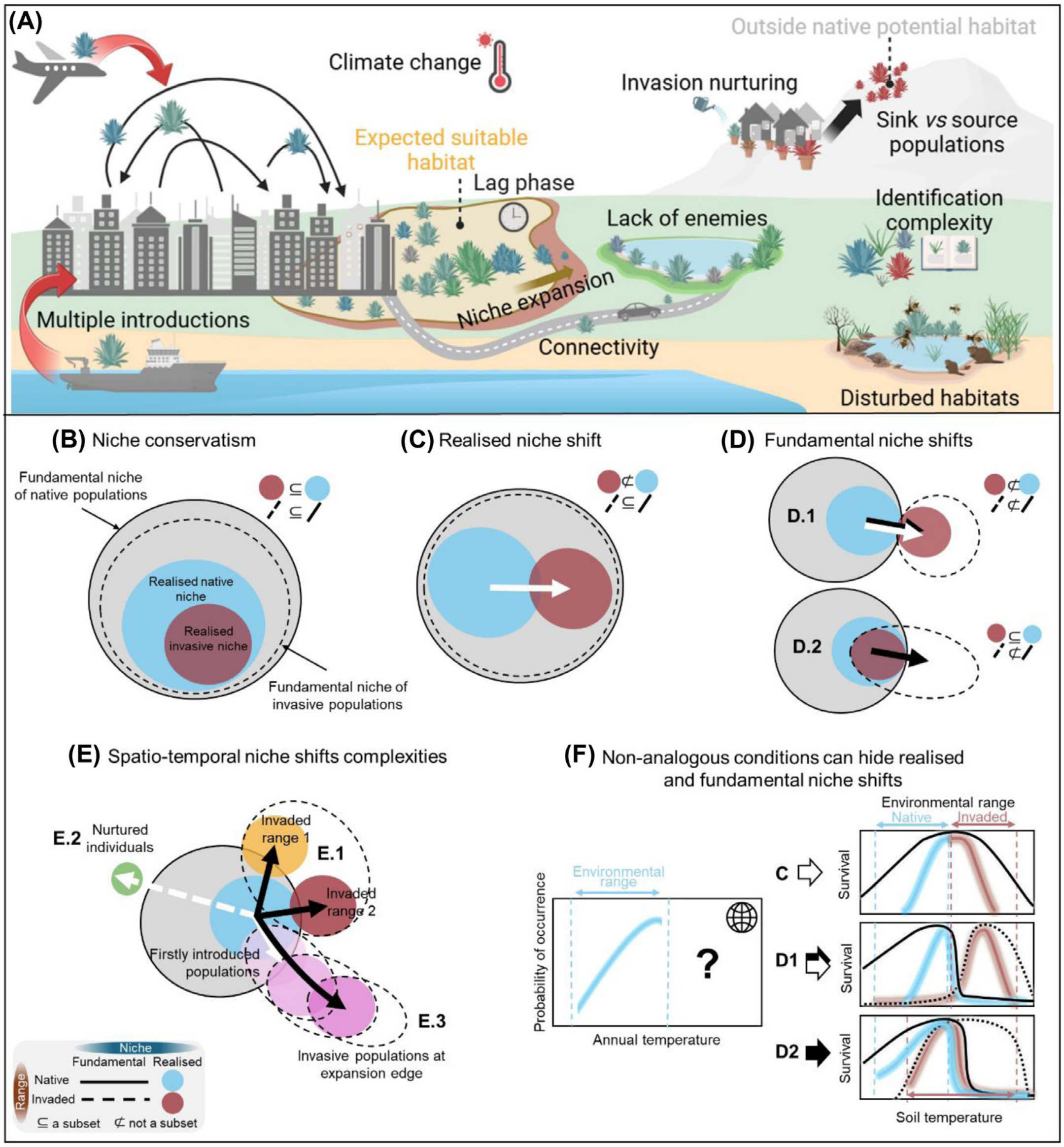

Figure 1. Schematic representation of the spatiotemporal complexities of invasive species distributions, from arrival to expansion. (A) Multiple introductions increase propagule pressure and facilitate invasions. Some species might not occupy their entire potential climatic niche due to a lag phase and may shift with climate change. Connectivity to disturbed habitats and the absence of natural enemies can further accelerate invasive spread. Invasion nurturing facilitates niche expansion into novel areas. Not all occurrences necessarily constitute established or source populations. Identification complexities may hinder invasive species registrations. For further details, refer to the text. (B–F) Niche conservatism and niche shifts (realised and fundamental). Figure conceptualisation adapted from Bates and Bertelsmeier (2021), with additional complexities of niche shifts in invasive species. (B) Niche conservatism – where the realised niche estimated from occurrences in the invaded range are a subset of the realised and fundamental niches in the native range. (C) Realised niche shift – when the realised niche in the invaded range is a subset of the fundamental niche but not of the realised native niche, indicating niche truncation or novel biotic interactions. (D) Two cases of fundamental niche shifts: the realised and fundamental niche from the invaded range are not a subset (D1) or do not fully overlap (D2) with the native fundamental niche. The latter pattern is observed when invasive populations establish in regions with the same environmental conditions as the native populations but have potential to expand further due to evolutionary processes. (E) Additional spatiotemporal complexities of invasive niche shifts: (E1) different invaded ranges (red and yellow) exhibit distinct realised niches while sharing a common fundamental niche. (E2) Species occurrences in the invaded range extend beyond the macro-environmental conditions of the species' fundamental niche (green). This phenomenon may result from records in arboretums, botanical gardens, zoos or sink populations, i.e. nurtured individuals. (E3) Realised and fundamental niche temporal shifts follow the invasion progression (pink), with niche shifts occurring primarily at the edges of the species' invaded range. (F) Realised niche estimated using occurrence data from the native range (left panel) or field data on the native (blue) and invasive (red) environmental ranges (realised niche in the right panels), may not represent the full fundamental niche (black for native, dashed for invasive) due to niche truncation, and thus niche shifts cannot be distinguished. Capital letters represent the niche shift type described in previous panels.

BOX 1. Spatiotemporal complexities of the Cape fig invasion – a case study.

The invasive Cape fig *Carpobrotus edulis* is a succulent clonal plant native to the Cape region of South Africa. Its creeping stems form dense mats, enabling it to thrive in diverse environments (Wisura and Glen 1993). *Carpobrotus edulis* has successfully invaded Mediterranean climate regions, spreading extensively across coastal sand dunes, rocky coasts and sea cliffs in Europe (Campoy et al. 2018). This invasion negatively impacts native communities, reducing local richness and diversity (Vilà et al. 2006, Santoro et al. 2012, Sarmati et al. 2019). Additionally, *C. edulis* modifies soil conditions through necromass production, altering pH, moisture, nutrient content and microbial activity (Santoro et al. 2011, Novoa et al. 2013, Vieites-Blanco and González-Prieto 2018). Here, we selected ten examples of mechanistic determinants behind *C. edulis* success that limit the predictive capacity of correlative SDMs (numbered in Fig. 2). (1) Ornamental interest increases propagule pressure both within and outside its suitable range. For instance, in its native range, the species experiences average annual rainfall under 500 mm but it has invaded areas like Galicia (NW Spain), which receive 1228 mm (photo: E. Fenollosa). The presence of this species in Europe, and particularly in regions with high precipitation, reflects the colonial legacy of British, Spanish, Portuguese, and Dutch empires, which structured alien floras worldwide (Preston and Sell 1988, Lenzner et al. 2022). (2) The species' presence is associated with habitat disturbance (Lechuga-Lago et al. 2017). (3–4) Differential stress responses have been observed between native and invasive populations under varying water and temperature conditions (photos from Fenollosa and Munné-Bosch 2019a, Campoy et al. 2021). (5) Realised niche shift towards colder regions and fundamental niche shift towards increased chilling sensitivity was found between European (invaded) and the native ranges (Fenollosa and Munné-Bosch 2019a). (6) Multiple genetic clusters have been identified within invaded ranges (Novoa et al. 2023). (7) Large intraspecific variability in seed production has been observed over short distances (Fenollosa et al. 2021). (8) Populations form persistent soil seed banks with different longevities (Fenollosa et al. 2020). (9) Facultative crassulacean acid metabolism (CAM) and photo-assimilates and nutrients exchange between independent units within clonal individuals (i.e. physiological integration) enable resilience to resource heterogeneity (Roiloa 2019). (10) Growth and death cycles regulate the exponential impacts of the invasion (Fenollosa et al. 2016). This case study illustrates the spatiotemporal complexities of invasion, demonstrating the limitations of correlative SDMs and emphasising the importance of mechanistic approaches.

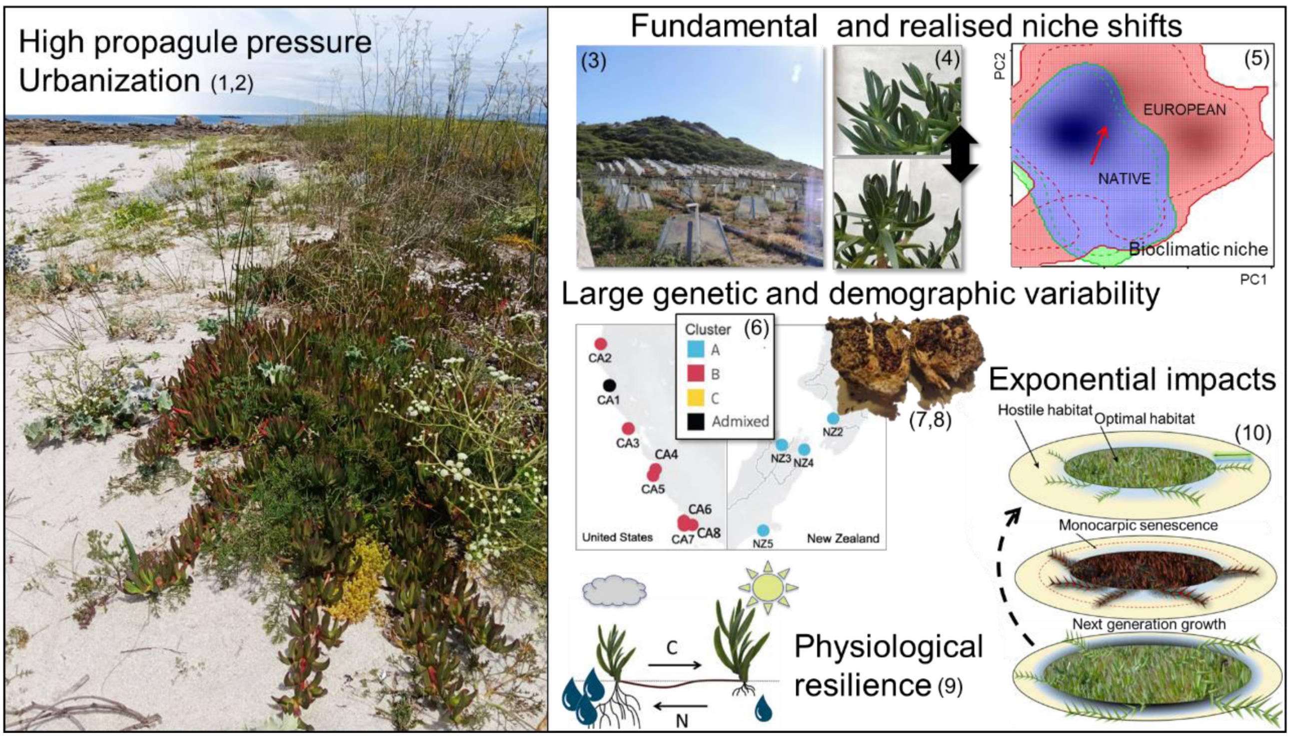

Figure 2. Ten documented mechanisms underlying the successful invasion of the Cape fig *Carpobrotus edulis*, highlighting the elements that shape its distribution, hindering accurate forecasts using correlative SDMs. Pictures credit is acknowledged in Box 1.

site accessibility (e.g. roads, urban areas; Kizuka et al. 2014, Botella et al. 2020). Species records (i.e. occurrences) as mostly found in global databases (Zizka et al. 2019) typically also fail to indicate whether observations represent cultivated or natural populations (López-Guillén et al. 2024) as well as highly-invasive or sink populations, potentially leading to misinterpretations of habitat suitability and invasion risk (Hui 2023).

Niche shifts: invasive species might colonise conditions outside their native realised and fundamental niches

After arriving in a novel environment, one of the primary factors determining a species' establishment is habitat suitability (Weiher and Keddy 1995, Broennimann et al. 2021). Habitat suitability depends on the climate, resource availability, and disturbances regimes (Hirzel and Le Lay 2008). Invasive species often thrive in environments resembling their native habitats (i.e. environmental matching) but with fewer natural enemies (Keane and Crawley 2002, DeWalt et al. 2004), allowing rapid spread to potentially new conditions outside their native niche (Broennimann et al. 2007). During invasion, invasive species can experience different types of niche shifts impacting SDMs predictions (Guisan et al. 2014; Fig. 1B–F).

When the niche occupied by the species in the invaded range remains similar to the one in the native range (i.e. across all populations in each range), the species is said to exhibit niche conservatism (Peterson 2011), suggesting that its ecological requirements remain unchanged (Bates and Bertelsmeier 2021; Fig. 1B). On the contrary, if the niche in the invaded range changes compared to the native one, e.g. by expanding or retracting its niche limits, it exhibits a niche shift (Fig. 1C–E; Broennimann et al. 2007, 2012, Guisan et al. 2014, Bates and Bertelsmeier 2021). As Pearman et al. (2008) noted, such niche shifts might be due to: 1) evolutionary processes that lead to a differentiation of the fundamental niche during the invasion process (i.e. a fundamental niche shift; Treier et al. 2009, Alexander and Edwards 2010; Fig. 1D) and/or 2) ecological processes, such as dispersal limitations, change in biotic interactions, and anthropogenic influences on habitat availability which make the species occupy a different subset of its fundamental niche (than in the native range), even if the fundamental niche is conserved (i.e. a realised niche shift; Fig. 1C–F; Van Valen 1965, Bolnick et al. 2007, Broennimann et al. 2007). Fundamental niche shifts are a result of rapid adaptation processes associated with the lack of natural enemies, founder effect and/or genetic drift (Eckert et al. 1996, García-Ramos and Rodríguez 2002), and play a critical role in invasive success (Pearman et al. 2008, Colautti and Barrett 2013, Fenollosa and Munné-Bosch 2019a, Campoy et al. 2021; Box 1).

The phenomenon of observing species only within a subset of their fundamental niche (Fig. 1F) can result from limited habitat availability (Pearman et al. 2008, Petitpierre et al. 2012, Guisan et al. 2014), biotic interactions (Tingley et al. 2014), dispersal limitations (Qiao et al. 2017), anthropogenic influences on habitat availability (Faurby and Araújo 2018, Pang et al. 2022), or a combination of those. It is noteworthy that some authors use the term 'niche truncation' when 1) a restricted geographic extent is used to fit the model only capturing a part of the species realized niche (Chevalier et al. 2021a, 2022, Adde et al. 2023, Goicolea et al. 2025), or 2) a species is pre-adapted to environmental conditions that are not found in its current native range, but could be revealed by climate change (Chevalier et al. 2024a).

Hence, using only occurrences from the native range (as well as occurrences from sink populations in the invaded range) to fit a SDM in the invaded range is discouraged as they do not necessarily reflect species potential in the invaded range (Barbet-Massin et al. 2018, Qiao et al. 2019, but see Broennimann and Guisan 2008), and might hide niche shifts (Fig. 1F). Predicting species distributions outside the native range or to novel environmental conditions such as climate change (i.e. predicting to non-analogous conditions; Elith 2017, Chevalier et al. 2024a), requires a full understanding of species' physiological limitations and the processes behind niche changes (Fig. 1F; Kearney et al. 2009, Guisan et al. 2014, Elith 2017, Briscoe et al. 2023).

Non-equilibrium distribution: lag-phase, management and range expansion

Time plays a complex and non-linear role in defining the distribution of invasive species (Theoharides and Dukes 2007, Broennimann et al. 2014, Robeck et al. 2024). After a species arrives in a novel environment, the lag period before noticeable population growth varies significantly, creating an invasion debt (González-Moreno et al. 2017, Evers et al. 2021, Duncan 2021). This establishment lag phase is influenced by certain functional traits (Robeck et al. 2024). Once established, species with high fecundity and adaptability tend to colonise new areas more rapidly (Capellini et al. 2015, Allen et al. 2017). Climate shifts, land-use changes, management actions or resource availability can trigger sudden outbreaks, accelerating the spatial and temporal spread of invasive species (Broennimann et al. 2014). Additionally, conservation actions – such as eradication efforts or habitat restoration – can further influence invasion dynamics (Pyšek and Richardson 2010).

Populations within the invaded range may further be influenced by different drivers of distributions (i.e. intraspecific niche variation). High genetic variability within invaded ranges due to multiple introductions (Smith et al. 2020), along with hybridisation and rapid adaptation, can result in population genetic differentiation within a single species' invaded range (Pearman et al. 2008, 2010, Colautti and Barrett 2013; Fig. 1E.1). Rapid adaptation during range expansion may lead to genetically distinct populations (Alexander and Edwards 2010, Szewczyk et al. 2019), causing fundamental niche shifts and subsequent range expansion within the invaded range (Cordier et al. 2020; Fig. 1E.3). Such local adaptation can lead to local populations having distinct physiological limits to environmental conditions (e.g. temperature), which raises questions about applying a single response curve per predictor to the whole of a species' range (Kolbe et al. 2010). As a consequence, SDMs calibrated with, e.g. early invasion occurrence data or recently naturalised populations (which did not have time to adapt), could result in underestimations of the invasive potential compared to those using established populations (Dullinger et al. 2009, Václavík and Meentemeyer 2009).

Human assistance to exotic species outside their climatic niche can also promote invasive populations differentiation and fundamental niche shifts within the invaded range (Thompson 2005, Ellstrand et al. 2010; Fig. 1E.2). We propose naming this phenomenon 'invasive nurturing' (i.e. assisting organisms outside their climatic niche opening the possibility for adaptation). Botanical gardens exemplify this phenomenon, assisting species to survive outside the environmental conditions of the native range (Klonner et al. 2019, Junaedi et al. 2021, Ni and Hulme 2021, Culley et al. 2022) and then adopt invasive behaviours (Shackleton et al. 2020). Economic interests, such as the ornamental trade, contribute to this process (Beaury et al. 2021, Bradley et al. 2023).

Populations at the edges of a species' range – where physiological stress, genetic drift, expansion load, and swamping gene flow from range interiors are more pronounced – add further uncertainty to distribution models (Gaston 2009, Sexton et al. 2009, Collart et al. 2021, Song and Li 2023). Probably due to the high selection pressure, invasive plants often exhibit higher growth rates in edge populations compared to central populations (Gruntman and Segev 2024). Aligned to this, the centre–periphery hypothesis posits that demographic performance declines from the centre of a species' range towards its edges (Brown 1984). While this hypothesis has been supported in some cases (Bontrager et al. 2021, Perez-Navarro et al. 2022), calls for its re-evaluation highlight the need for empirical studies, particularly for invasive species (Purves 2009, Csergő et al. 2017, Pironon et al. 2017, Chevalier et al. 2021b, Kunstler et al. 2021).

Hybridisation, genetic admixture and genetic drift might hinder invasive species identification

Crypticity in species identity within invaded ranges (Jarić et al. 2019) or during range expansion (Rosche et al. 2025) represent a significant source of observational bias, affecting the outputs of correlative SDMs. Hybridisation and strong genetic admixture because of the fast adaptation processes of invaders at novel environmental conditions often hinder a clear identification (Hodgins et al. 2025). Examples include the native-invasive admixture of common reed *Phragmites australis* (Pyšek et al. 2018), genetic clusters of the Cape fig *Carpobrotus edulis* (Campoy et al. 2018, Novoa et al. 2023), shifts in cytotype frequency in the spotted knapweed *Centaurea stoebe* (Treier et al. 2009, Rosche et al. 2025), the enigmatic complex of Lantana *Lantana camara* (Goyal and Sharma 2015), conflicting morphological descriptions of the peppermint shrimp *Lysmata vittata* (Aguilar et al. 2022), and confusion between devil's backbone *Kalanchoe daigremontiana* and its invasive hybrid *K.* × *houghtonii* (Herrando-Moraira et al. 2020).

Mechanistic niche models: forecasting species' potential from physiological limitations

Given that correlative SDMs may be unreliable, particularly for species with non-equilibrium distributions or source-sink dynamics (Briscoe et al. 2019, Lee-Yaw et al. 2022), alternative or complementary approaches are needed to predict invasive species distributions, determine potential habitats, and understand eco-evolutionary processes under climate uncertainty. Accordingly, ecologists are increasingly incorporating biological processes into distribution predictions.

There are a range of process-explicit (also termed 'process-based' or 'mechanistic') models that directly incorporate factors such as physiology, dispersal, demography evolution and biotic interactions (definition and classification of process-explicit model types can be found in Briscoe et al. 2019 and Urban et al. 2022). Here, we focus on models that capture physiological constraints by explicitly incorporating the mechanistic links between the functional traits of an organism and its environment (Kearney and Porter 2009). These models are referred to by a range of terms including ecophysiological models, biophysical models, mechanistic SDMs or mechanistic niche models, with terminology depending partially on the extent to which mechanistic links are identified via experimental data (e.g. on physiological tolerances, thermal performance) or calculated using first principles (Gates 1980). For simplicity, we refer to these collectively as mechanistic niche models (MNMs, following the definition in Briscoe et al. 2019) hereafter, but we will highlight the implications and potential challenges of differences in parameterisation. Despite sharing the word 'mechanistic', note that 'mechanistic models' (= process-explicit) is a broad term to describe models that incorporate mechanisms or processes to explain species distributions, and 'mechanistic niche models' is a subgroup of models that incorporates species' mechanistic links behind physiological constraints (Briscoe et al. 2019).

We focus on MNMs because, by definition, they are grounded in the species' fundamental niche, making them particularly suited for predicting the potential distribution of invasive species, including under climate change. MNMs use experimental data or calculated physiological limitations – such as thermal limits and water requirements – to define species' range limits and project distributions (Kearney and Porter 2009, Evans et al. 2015). By incorporating biological mechanisms from experimental data including physiological tolerances (e.g. thermal limits, growth rates) and demographic rates (e.g. survival and fecundity), MNMs provide a nuanced understanding of species distributions independent of recorded occurrences. In principle, this would allow predictions under novel environmental conditions, and could aid conservation and management efforts, such as identifying critical thermal thresholds or optimising invasive species management.

Building MNMs demands a substantial amount of detailed, species-specific empirical data linked to relevant environmental variables. Physiology has been proposed as a key component of more 'mechanistic' species distribution models (Schwinning and Parsons 1996), but the need for combined expertise in modelling, demography, and environmental physiology has hindered the widespread adoption of MNMs (Kearney and Porter 2009, Buckley et al. 2010, Kearney et al. 2012, Woodin et al. 2013). Kearney and Porter (2009) identified a major challenge in linking behavioural, morphological, and physiological traits with GIS datasets on climate and terrain. To address this challenge, they proposed using biophysical ecology, a field that applies thermodynamic principles to organisms to derive mechanistic models of their physiological processes and responses (Gates 1980). Biophysical models require data on species' morphological, physiological and behavioural traits, and can be parameterised using data from a range of sources including museum specimens, behavioural observations, physiological experiments and allometry (Riddell et al. 2023). Whereas biophysical models have mainly been used in ectotherms, their use in endotherms is growing (Angilletta 2009, Briscoe et al. 2023). Similarly, dynamic energy budget models, which can be integrated with biophysical ecology to more fully capture environmental constraints on animal fitness (Kearney et al. 2010), have also been proposed for modelling resource allocation and species distribution in plants (Schouten et al. 2020, Russo et al. 2022).

Key data inputs of MNMs include physiological parameters, such as metabolic rates, thermal tolerances (upper thermal limit, lower thermal limit, activity window), developmental rate, hypoxia tolerance and growth rates under environmental gradients (Evans et al. 2015). However, physiological constraints may occur in a hierarchical manner, with some processes (or during certain developmental stages) being more sensitive to environmental change. For example, in some species, locomotion and reproduction are thermally constrained, whereas survival is possible to a wider range of temperatures (Buckley and Kingsolver 2012). Overall, data requirements for MNMs vary significantly across different organisms, as different species demand unique physiological, demographic, or environmental datasets to accurately capture environmental constraints.

While MNMs have primarily focused on environmental variables such as temperature, other key mechanistic elements that shape species distributions can also be incorporated. Although temperature significantly influences species performance, species-specific critical temperatures often fail to fully explain biogeographical patterns (Sunday et al. 2012, Chevalier et al. 2024b). Other global gradients – such as oxygen levels, light availability, pressure, pH, and water balance – play vital roles in shaping species distributions. These factors covary with latitude, elevation, and ocean depth, and species exhibit strong physiological and behavioural adaptations to these abiotic variables within their historic ranges (Spence and Tingley 2020). A greater focus on these underexplored variables into MNMs could enhance the models' ability to predict distributions across diverse environments and under changing climate conditions (Kearney et al. 2018, Telemeco et al. 2022).

MNMs mark a significant advancement in ecological modelling by linking physiological processes with species distributions to deliver biologically grounded predictions, allowing in principle for more robust projections under novel environmental conditions, such as those induced by climate change or species invasions. By simulating species interactions with key environmental factors – such as temperature, water availability, and other gradients – MNMs enhance our understanding of the fundamental niche. Despite their substantial data and parameterisation requirements, making them currently difficult to apply to large numbers of species (as SDMs can do, Adde et al. 2023), these models can provide unparalleled insights into ecological dynamics. Consequently, MNMs are essential for advancing ecological research and optimising conservation and management strategies in a rapidly changing world (Kearney and Porter 2009, Elith et al. 2010, Higgins et al. 2020).

MNMs on invasive species

Relative to SDMs, MNMs are still not widely used, but modelling invasive species distributions has been one of their main applications (Briscoe et al. 2019). To explore the number of studies that have attempted to predict invasive species distributions from physiological limitations, understand the diversity of nomenclature and model types, as well as types of empirical data used to parameterise the model, we performed a systematic review of published studies using MNMs in invasive species worldwide. Briefly, we based our search on Briscoe et al. 2019 search terms to obtain three types of process-explicit models: MNMs, demographic distribution models (DDMs) and individual-based models (IBMs), combined with filters to detect studies with invasive species. Although DDMs and IBMs were out of the scope, we included them in the search terms to check if some of them could also be categorized as MNMs. This was common for IBMs, which simulate populations considering discrete individuals each with a set of attributes. We included IBMs that accounted for individual's performance in response to environmental constrains from experimental data, as well as DDMs that were fitted using experimental data (see search terms and further detail in the Supporting information).

Mechanistic niche models have been used to a limited extent. In our systematic review, we found only 53 articles that applied MNMs to invasive species, with the first article published in 2007 (Fig. 3, Supporting information). This relatively low number highlights the challenges of gathering the complex data required to construct MNMs and apply them effectively in the field. Additionally, the lack of unified nomenclature for naming these models across studies further complicates their identification. In this regard, our systematic review revealed diverse model nomenclature usages when building MNMs with invasive species. Across the 53 articles, authors named MNMs as physiologically based (Higgins and Richardson 2014), biologically informed (Lozier and Mills 2011), biophysical (Tingley et al. 2014), temperature-driven

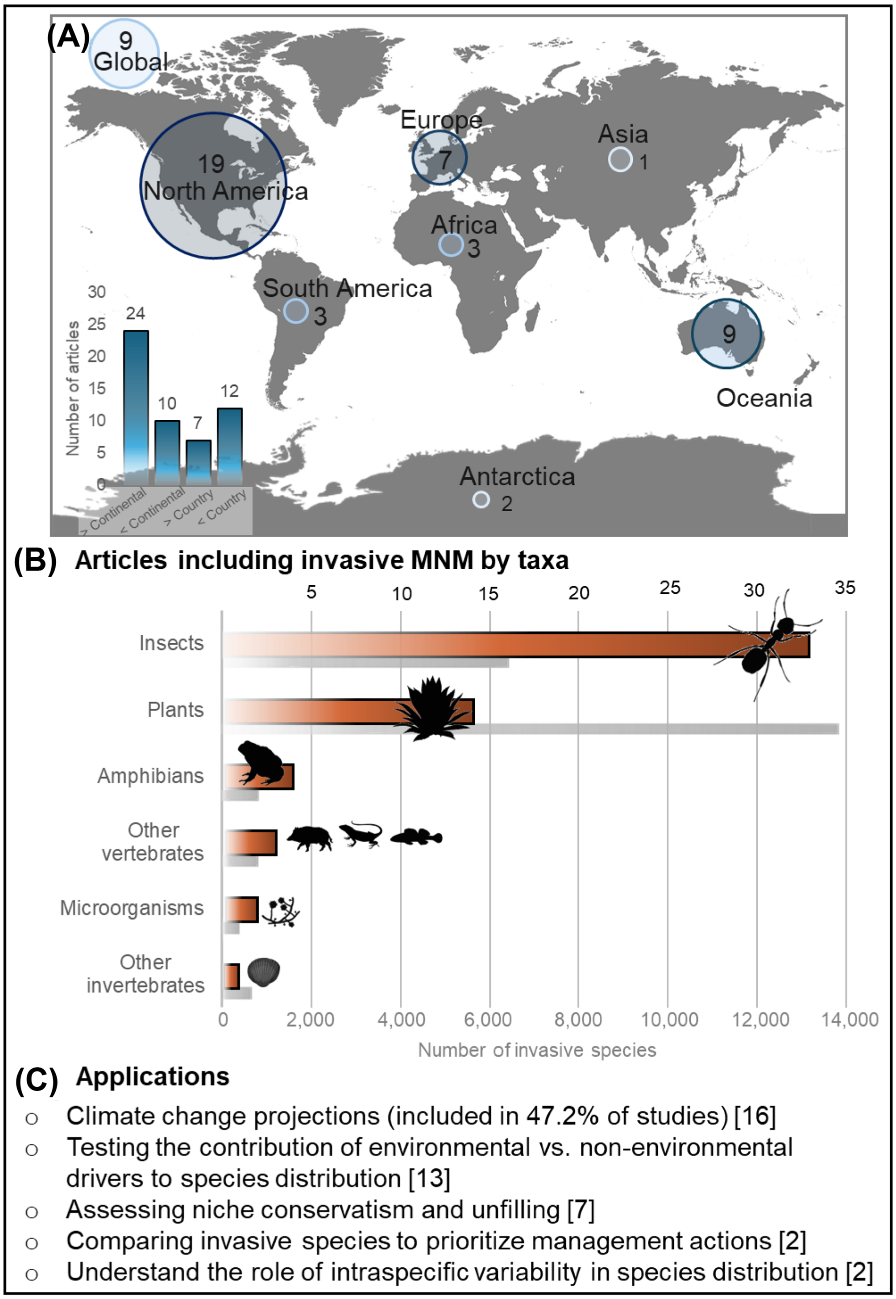

Figure 3. Summary of the systematic review performed to evaluate the usage of mechanistic niche models with invasive species. (A) Continental distribution of MNMs with invasive species. Bubble size and blue intensity reflect the number of articles in each continent. On the left bottom, scale of the articles. (B) Taxonomic group used for the examination of invasions using MNMs (brown), and global number of invasive species according to IPBES 2023 (Roy et al. 2024) (grey). Note that each series has its own axis, reflecting no-proportionality between variables. Even though insects are most commonly the focus of invasive MNMs, the number of invasive plants is much higher than the number of insect invasive species. Species icons obtained from BioRender. (C) Applications of MNMs for invasive species. In brackets, the number of articles.

(Logan et al. 2007), ecophysiological (Ginal et al. 2021), process-based (Gutierrez et al. 2008), mechanistic phenology (Iwamura et al. 2020), and phenotypically explicit model (Brass et al. 2024). Surprisingly, we found that a full description of physiological processes that constrain species performance under different environmental conditions was rare. Instead, researchers typically include a subset of key processes or physiological constraints. We identified several pre-built frameworks that can be broadly applied to specific groups of organisms, such as the CLIMEX model (Ponti and Gutierrez 2023). However, some of these pre-built frameworks can optionally use species occurrence data from the field for parameterisation, which then captures the realized rather than the fundamental niche. When this is the case, they thus constitute hybrid approaches rather than strictly mechanistic models. Considering the strong data requirements to parameterise MNMs, we nevertheless decided to include and discuss benefits and limitations of all these approaches, which in some cases will not be suited to understand invasive species potential distribution under novel environmental conditions.

When classifying the MNM studies in our review by modelled taxonomic groups, over 50% focused on insects while nearly 20% addressed plants (Fig. 3). Invasive insects such as the tomato pinworm *Tuta absoluta* (Ponti et al. 2021, Early et al. 2022, Ponti and Gutiérrez 2023), mosquitos *Aedes* sp. (Iwamura et al. 2020, Pasquali et al. 2020, Brass et al. 2024) and plants, such Ambrosia *Ambrosia artemisiifolia* (Chapman et al. 2014, 2017, Leiblein-Wild et al. 2016) have been frequent subjects of these models due to their health, economic and ecological impacts and ability to rapidly colonise new environments. The extensive use of MNMs in insect studies is primarily due to these species' strong dependence on temperature, as well as their potential to act as disease vectors (Rebaudo and Rabhi 2018). Besides insects and plants, four articles reported MNMs with amphibians (Kearney et al. 2008, Kolbe et al. 2010, Tingley et al. 2014, Ginal et al. 2021), two with microorganisms (virus: Taylor et al. 2019, and fungus: Deiß et al. 2024), three with other vertebrates (a mammal: Tablado and Revilla 2012, a reptile: Lin et al. 2019, and a fish: Zhu et al. 2020), and one study with a mollusc (Feng et al. 2020) (Fig. 3, Supporting information).

Of the 53 articles found, 25 (47.2%) included projections of invasive species distribution under climate change scenarios, while the remainder focused on present environmental conditions. However, the aim of these studies was not solely to project species distribution under climate change conditions, but other applications. The second most common application of MNMs was to explore the contributions of environmental versus non-environmental drivers in shaping invasive species distributions (Fig. 3). To do so, authors built both correlative models and MNMs and contrasted the resulting projections. One example of this is the study of the sub-Antarctic insect, brachypterous midge *Eretmoptera murphyi* by Pertierra et al. (2020). In this work, a MNM was parameterised from vital rates as a function of temperature obtained after laboratory experiments where survival, growth and fecundity were monitored in larvae exposed to 0, 2, 4, 6 and 8°C for 30 days, simulating the austral summer. The contrast of this MNM to a correlative SDM that considered a regional human footprint map as covariates revealed the high potential for the species to expand its invaded range and how its current distribution is shaped by human presence.

Other applications of MNMs to invasive species included: comparing multiple invaders' potential distribution to assist management (Gutierrez and Ponti 2013), testing niche conservatism or niche shifts between invaded and native ranges (Tingley et al. 2014) and understanding the role of intraspecific variability in species distributions (Kolbe et al. 2010). In some cases, both native and invasive species distributions were parameterised, such as the pathogen Bsal *Batrachochytrium salamandrivorans* with the threatened native fire salamander *Salamandra salamandra* to determine extinction risk (Deiß et al. 2024). In addition, some articles also used MNMs to predict invasion dynamics (Fadda et al. 2024, Walter et al. 2024), but to do so, MNMs were coupled with occupancy data to predict spread. This was the case for Walter et al. (2024), who used the temperature-dependent developmental performance of the spongy moth *Lymantria dispar dispar* as a covariate within a Bayesian occupancy model that considered tree canopy cover, local diffusive spread, habitat connectivity and population density from pheromone-baited traps. Another study predicted invasion spread from physiological data by parameterising the model with time-dependant rates (Hartley et al. 2010). In Hartley et al. (2010), a degree-day model of development was used to model growth and distribution of the Argentine ant *Linepithema humile* in Hawaii, predicting the rate-of-spread and future range expansion.

Our review identified several approaches used to meet data requirements for constructing MNMs. Thermal tolerance was the most frequently used metric to build response curves for invasive MNMs (Ginal et al. 2021 in an invasive frog, Brass et al. 2024 for an invasive mosquito). Following temperature, the relationship of temperature with species phenology or developmental rates was the second most common studied process to parameterise MNMs. Some examples include modelling the timing of the breeding season in invasive rabbits (Tablado and Revilla 2012), or Ambrosia's cold limitation by phenology (Chapman et al. 2014). Contrastingly, Zhang et al. (2021) built an MNM with soil water and nutrient requirements data from a microcosm experiment with cogongrass *Imperata cylindrica*. Beyond environmental variables, other mechanisms that have been included when building MNMs in invasive species are multiple trophic systems (e.g. with the invasive yellow star-thistle in Gutierrez et al. 2008), demographic stochasticity (e.g. with the invasive European rabbit in Tablado and Revilla 2012) or evolutionary dynamics (e.g. with the dengue mosquito *Aedes aegypti* in Kearney et al. 2009). Whilst survival was most commonly the focus of the reviewed studies, some studies incorporated reproductive components or specific metabolites levels to reflect species performance. For example, corticosterone levels influence avian range limits (Treen et al. 2015) or glycogen stores reflect the optimal status for aquatic ectotherms (Maazouzi et al. 2011).

Whereas some studies based the MNM on energy budget models (or more generally, resource allocation models; Higgins and Richardson 2014, Leiblein-Wild et al. 2016), others were built from laboratory tests conducted under a limited number of experimental conditions (e.g. five different temperatures; Pertierra et al. 2020, Fadda et al. 2024) or combined both via energy-mass balance equations (Kearney et al. 2008, Kolbe et al. 2010). All modelling approaches result in a model where the response, an individual's performance, is a function of environmental conditions. Whereas laboratory-based models are constrained by the data used for parameterisation (e.g. specific laboratory-tested temperatures, life stage selected), resource allocation models are limited by the equations used, which are based on prior knowledge of the species. Regarding laboratory-based models, Fadda et al. (2024) modelled Ambrosia beetle *Xyleborus bispinatus* performance by fitting a convex function to growth rate data obtained from individuals exposed to a temperature gradient (17, 20, 26, 29, 35°C) over 36 days. Similarly, Pertierra et al. (2020) exposed midge larvae to 0, 2, 4, 6 and 8°C for 30 days, while Lin et al. (2019) subjected invasive lizard adults to four temperature groups: 10, 12, 14 and 16°C for 28 days. In contrast, Feng et al. (2020) used a plateau model, representing the abiotic niche with three connected segments of differing slopes. This model was fitted with data from various experiments conducted at different temperature intervals.

On another hand, MNMs that use energy–mass balance equations can take multiple complexity levels (Briscoe et al. 2023). An example of an energy budget model is the MNM of the cane toad *Rhinella marina* in Australia. For this species, core body temperature was modelled by solving a steady-state energy balance equation (Kearney et al. 2008). While such approaches can predict responses under all potential combinations of conditions, they require extensive species-specific knowledge. For instance, Kearney et al. (2008) incorporated data on morphological (e.g. surface–body mass functions, the distance of an average adult from the ground), physiological (e.g. lethal body temperatures and thermal dependence of development rates for eggs and larvae, metabolic rates, thermal dependence of movement in adults), and behavioural (e.g. activity, microhabitat selection, postural changes) traits as well as simulations of water temperatures in ponds with different configurations.

Representativeness of measured individuals must be considered when building MNMs, as failure to capture variation between or within populations might limit our ability to accurately model invasive species' dynamics. Kolbe et al. (2010) showed that low temperature tolerance is not a constant trait across the invaded range of the cane toad, meaning measurements of this trait from individuals from a single population would not represent the potential expansion of the species. To enhance representativeness, some works considered using multiple genotypes (Chapman et al. 2017), selected a source population likely to be the introduction point (Coulin et al. 2019) or used at least a second generation to avoid maternal effects (Pertierra et al. 2020).

Factors limiting species distributions are not always replicable under controlled conditions, necessitating alternative approaches. This challenge is particularly relevant for species with low growth rates (e.g. trees) or those whose distributions are shaped by the interaction of multiple factors. For example, there has been recent criticism of combining physiological thermal limits obtained from physiological experiments with macroclimate data to capture species distribution limits, particularly at lower temperatures, since adaptive and/or facilitative mechanisms including behaviour often mean that macroclimate data do not reflect conditions species experience in the wild (Chevalier et al. 2024b). Unlike forward fitting (experimentation of individual's responses to the environment), inverse fitting (use of species occurrence or performance data from across areas with different environmental conditions to identify likely parameter values) can capture species responses to multiple environmental conditions simultaneously or to wider ranges, for example beyond fixed temperature regimes (Evans et al. 2016). Characterising species performance across latitudinal, altitudinal, or moisture gradients has been employed to parameterise some parts of distribution models for invasive species (Augustinus et al. 2020, Pasquali et al. 2020). However, it is crucial to note that parameterising a model with inverse fitting approximates the realised niche rather than the fundamental niche. Given that the realised niche of invasive species may not fully represent their capacity to colonise further environmental regions, projections based on such models are likely to be biased, limiting their reliability for predicting future distributions.

Another method used to integrate more environmental conditions rather than a single environmental variable is the one taken by Merow et al. (2017), who modelled the invasive garlic mustard *Alliaria petiolata* and Japanese barberry *Berberis thunbergii* by collecting demographic data from a series of transplant plots across diverse environments within the invaded range. This approach (defined as a demographic distribution model by the authors) is closer to a MNM in that it captures the species' response to a broader range of environments, but it is restricted to the current environmental conditions in the selected range. In addition to the fact that field data are often available only from a subset of the environments available in the invasive range, models parameterised using field data often implicitly capture the effects of biotic interactions, and thus do not represent the fundamental niche. Experimental design and data parameterisation must be carefully designed according to the study aim and species status.

During the filtering phase of our systematic review, we identified several articles that integrate both physiological limit data and species occurrence records (hybrid models). Depending on how these models are parameterised, they may either inherit the limitations of correlative SDMs or align more closely with MNMs. CLIMEX was the most frequently used pre-built framework in the reviewed studies, appearing in 13 of the 53 articles, mainly with insects (but see Webber et al. 2011, Shabani and Kumar 2015 for plants). CLIMEX is a commercially available software (Sutherst and Maywald 1985), specifically developed for modelling invasive species, which assumes a normalised concave growth response of species to various factors, with minimum, maximum and optimum values. In CLIMEX and some other prebuild mechanistic frameworks, reaction norms in response to environmental factors can be fitted with experimental data but also with species occurrences (Shabani and Kumar 2015), and only the first case will be a mechanistic approach (Ponti and Gutierrez 2023). Similarly, the usage of previously described thermal response curves (Walter et al. 2024) from populations from the native range might not represent the invasive individuals. Hybrid models might be appropriate when aiming to model invasion rates in data-limited contexts (Klonner et al. 2019, Rodríguez et al. 2019, Bosch-Belmar et al. 2021, Guillaumot et al. 2022, Tourinho and Vale 2023). For example, Hassall et al. (2025) demonstrated how a hybrid model combining an MNM with observed patterns of spread of the invasive Asian hornet *Vespa velutina* provided insights into the effectiveness of management measures implemented in Europe to limit the species range expansion.

Beyond CLIMEX, other pre-built frameworks being used for invasive species fall within a subset of MNMs that integrate species' thermodynamical relationships with their environment and includes the TTR (Thornley transport resistance) (Higgins and Richardson 2014, Higgins et al. 2020) or dynamic vegetation models such as LPJ-GUESS for plants (Leiblein-Wild et al. 2016), DBEM (dynamic bioclimate envelop models) for fishes (Zhu et al. 2020), and NicheMapper for ectotherms and endotherms (Kearney et al. 2008, Kolbe et al. 2010, López-Collado et al. 2013, Tingley et al. 2014, Strubbe et al. 2023). These models focus on simulating energy, resource transport, and physiological processes to estimate species performance and potential growth. A TTR model simulates the transport of nutrients, water, and other resources and tend to focus on quantifying the resistance to transport between tissues and ultimately estimate an individual's potential growth (Higgins and Richardson 2014, Higgins et al. 2020). LPJ-GUESS is a dynamic global vegetation model that simulates plant growth, competition, and ecosystem processes by integrating physiological traits, carbon allocation and environmental conditions (Smith et al. 2001). Similarly, NicheMapper is based on energy balance equations and is mainly applied to endotherms and ectotherms (Kearney and Porter 2020, Briscoe et al. 2023), but recently to leaves (Kearney and Leigh 2024). These biophysical models have been used mainly on invasive amphibians, and use detailed behavioural and physiological parameters such as activity, metabolic rates and survival, development or growth in response to body temperature, given that these taxa show strong dependence on temperature. Similar models not yet used in invasion research include: Phenofit (Chuine and Beaubien 2001), Sortie-ND (Canham and Murphy 2016), 3-PG model (Gupta and Sharma 2019) and AquaMaps (Kaschner et al. 2006).

Despite the high variation in model types and integrated processes identified in our review, the geographical distribution of studies was relatively limited. This geographical constraint might be due to the low number of MNMs, but the distribution is consistent with findings from other systematic reviews on correlative SDMs (Lantschner et al. 2018, López-Tirado and Gonzalez-Andújar 2023), where North America accounted for the highest number of invasive species MNM studies (Fig. 3). However, most MNMs were developed at global scales, spanning more than one continent. The strong data requirements for MNMs likely contribute to this inequality. Access to well-equipped laboratory facilities, experimental installations, computational centres or reference researchers, combined with large budget grants available in more privileged regions, disproportionately supports the development of MNMs in wealthier areas. Addressing this imbalance may require increased international collaboration and capacity-building efforts to ensure broader representation in MNM research.

Towards a unified framework for invasive mechanistic niche modelling

Despite several articles outlining standards, guidelines and key considerations for building and reporting SDMs (Araújo et al. 2019, Zurell et al. 2020, Sillero et al. 2021, Hui 2023, Davis et al. 2024, Soley-Guardia et al. 2024), a framework for designing, building, and reporting MNMs in invasive species is still missing. Related work includes a mechanistic modelling framework for developing eggs (Kearney and Enriquez-Urzelai 2023), a review of data used to parameterise biophysical models (Riddell et al. 2023), a unified modelling framework for invasive *Aedes* mosquitos (Da Re et al. 2022), a review on dynamic models for invasive species management (Buchadas et al. 2017), and a conceptual framework for the demographic niche concept (Pang et al. 2024b). We propose the following steps for building an MNM to determine the potential distribution of invasive species (Fig. 4).

1) Research aim. While clearly defining the research aim, management goal, or knowledge gap that we intend to address seems self-evident, we emphasise that these decisions will clearly influence MNM parameterisation. For example, MNMs are suitable for determining the potential for expansion of an invasive species toward specific environmental gradients, estimating distribution shifts with climate change, quantifying the niche overlap with threatened species or potential biocontrol agents, testing the contribution of environmental versus non-environmental distribution drivers and detecting niche unfilling (i.e. parts of the native niche not yet filled in the invaded range; Guisan et al. 2014; Fig. 3). Specifically for invasive species, framing the area of interest might determine key elements of the experimental design. For example, building an MNM to estimate an invader's potential to persist in a particular protected area requires response curves from genotypes growing nearby, which may limit transferability due to intraspecific niche differentiation (Pearman et al. 2010, Yates et al. 2018, Qiao et al. 2019, Collart et al. 2021, Anselmetto et al. 2025). MNMs can be built with varying levels of complexity and capture different types of constraints. Combined with knowledge of the species, the research aim can, for example, help us to distinguish whether the model should focus on upper thermal limits and water requirements (for assessing shifts to warmer climates), vital rates (to identify reproductive limits), specific microhabitats (to address targeted management outputs), specific performance metrics (to model energy requirements or dispersal potential), a single vulnerable life stage (to determine if the species is unable to survive in an area), or include all life stages, interaction

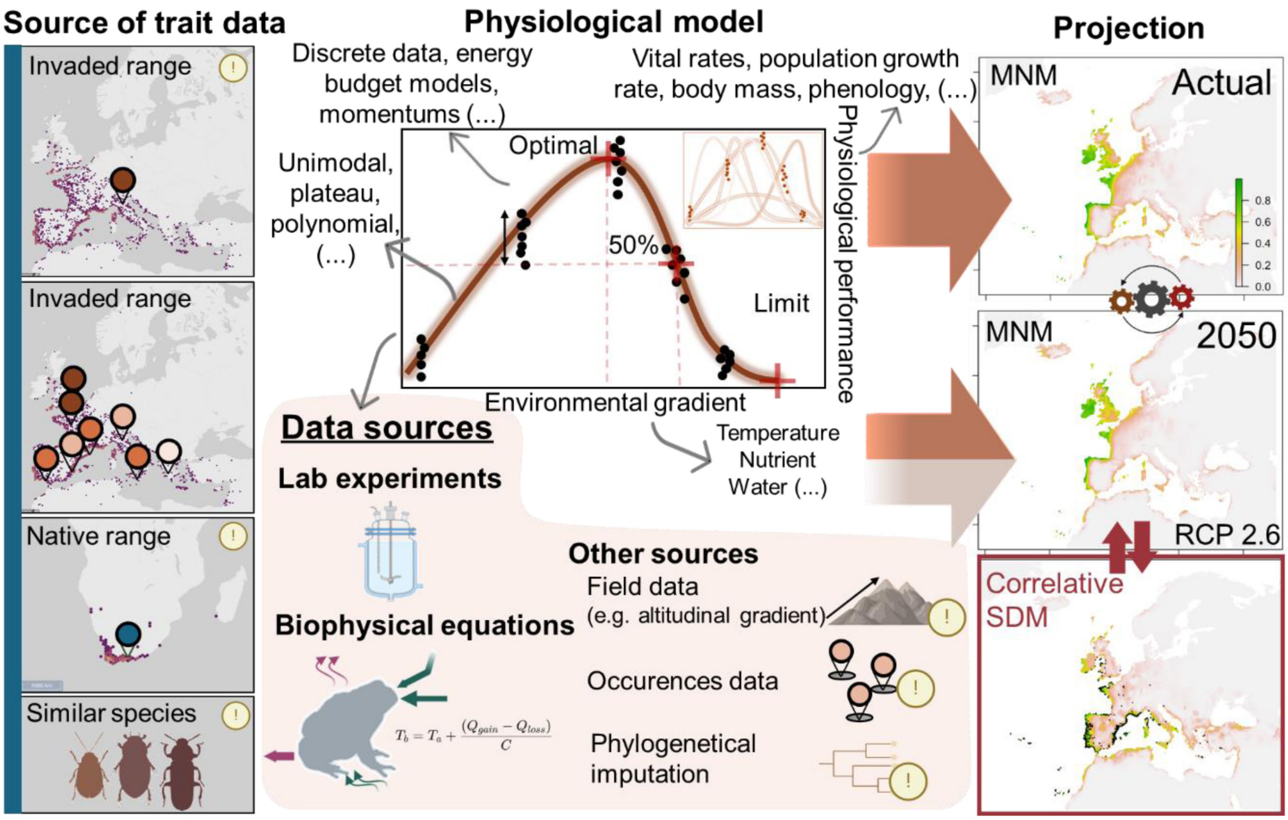

Figure 4. Elements to consider when building mechanistic niche models for invasive species, from four different strategies to select trait data (left boxes), the construction of the physiological model (including multiple data sources) and geographic projection under current or future conditions (right boxes), which might be contrasted with a correlative SDM. Trait data selection can include a single or multiple genotypes from the invaded or native ranges as well as the use of similar species. As discussed in the main text, selection strategies influence an MNM's potential. Exclamation signs (!) symbolise that by taking those approaches the model might not be suited for invasive species projections.

between environmental variables, competition and intraspecific variability (to understand the drivers of species persistence. Additionally, invasion dynamics – such as whether niches from native versus invaded ranges overlap, human-facilitated dispersal (invasion nurturing), and genetic variation – must be considered (Fig. 1).

2) Source of trait data. Prior to building a model, one or more genotypes must be selected according to the research aims, the degree and importance of the described genetic variability and considering the invasion dynamics literature. Figure 4 illustrates four common sources of trait data for invasive MNMs, each with advantages and limitations. Capturing intraspecific variability often requires sampling multiple populations within the invaded range (Gallien et al. 2012), as demonstrated by Kolbe et al. (2010) with the cane toad thermal tolerance. MNMs built with multiple genotypes address some of the correlative SDMs limitations for invasive species, since they can integrate niche shifts and range expansion processes, even if the invasion is in a lag-phase. When low variability across populations is observed or a trait is maintained in populations from native and invaded ranges, a single population would suffice. Sensitivity analysis can assist in delimiting the importance of intra or interpopulation variability (Strubbe et al. 2023). However, relying on a single population is likely to overlook range-edge processes. We recommend reporting the niche margin index (NMI; Broennimann et al. 2021), which quantifies a population's relative distance from the margin (either within or outside) of the species native realised niche, even in a climate change context (Pearman et al. 2024). When data are scarce, closely related species may serve as proxies (Wiens et al. 2010, Crisp and Cook 2012, James et al. 2021), or MNMs can be restricted to particularly sensitive developmental stages such as in some insect models, where only larvae are included on the MNM due to their climate sensitivity (Kingsolver and Buckley 2020).

3) Environmental drivers and response variables. Building MNMs typically requires measuring species responses to one or more environmental drivers over relevant intervals (e.g. 0–10°C), including the forecasted increase or decrease under climate change scenarios (e.g. +2°C). Whereas correlative SDMs rely on recorded occurrences to estimate the conditions where the species can persist, in MNMs the specific range of conditions over which species responses are measured can restrict model inferences. Environmental drivers are usually abiotic factors (e.g. temperature, humidity, soil moisture and atmospheric CO_2)

although biotic factors may be considered (Rogers et al. 2018). Selecting appropriate environmental variables required understanding the spatial and temporal resolution of factors limiting species survival, growth and reproduction (Spence and Tingley 2020). Biophysical models can help overcome data limitations associated with measuring species responses under the full range of possible conditions (Kearney and Porter 2009, Briscoe et al. 2023, Riddell et al. 2023). In addition to environmental variables (and their interactions), response or performance variables must be carefully selected. Performance measurements can include vital rates, development, metabolic rates or specific metabolite accumulation, and selection will depend on our research question, scale of the study, and type of organism. Multivariate approaches can be also considered to integrate tradeoffs in response curves (Fefferman and Romero 2013, Evans et al. 2015).

4) Physiological model: parameter estimation and model fitting. The full understanding of species' physiological limitations makes it possible to delimit the species' potential to respond to conditions that might not have been experienced in the native range or at any location at the current time (but to which the species is pre-adapted; Chevalier et al. 2024a). When using biophysical ecology, parameter estimation depends on model complexity (e.g. life-stages, energy and water balance, locomotion, etc.; see point 3). Selecting the appropriate equations for baseline physiological models depends on the species' physiology and can range from simple linear models to more complex non-linear equations that account for thresholds and tipping points in species' responses to environmental variables (Fenollosa and Munné-Bosch 2019b, Buckley et al. 2022). For thermal response curves, common modelling approaches include convex functions (Fadda et al. 2024), plateau models (Feng et al. 2020) and unimodal temperature-dependent developmental curves with a linearity zone before the optimal temperature (Rebaudo and Rabhi 2018). The choice of model should consider whether the aim is to estimate full-range responses, discrete conditions or specific physiological limits. At least five experimental conditions are typically used to fit thermal response curve (Lin et al. 2019, Pertierra et al. 2020, Fadda et al. 2024), but the experimental design will depend on the modelling aim. For instance, temporal regimes, such as constant versus fluctuating or extreme temperatures, must also be accounted for (Vajedsamiei et al. 2024). Beyond laboratory experimentation, some alternative data sources include phylogenetic imputation (James et al. 2021, Fadda et al. 2024) or the integration of expert knowledge (Murray et al. 2012).
5) Physiological model projection. Once response curves are fitted, physiological models must be translated into geographic projections. This usually requires estimating environmental conditions experienced by organisms at relevant temporal and spatial scales and translating physiological performance into a fitness metric that reflect species potential presence in a specific area. Environmental data choices in studies we reviewed varied considerably, ranging from monthly air temperatures (Tablado and Revilla 2012) to hourly soil temperatures (Hartley et al. 2010, Chapman et al. 2014). Microclimate models can improve data resolution (Meyer et al. 2023), aiding predictions of historic, current or future conditions while considering species behaviour and habitat use (Kearney et al. 2020, Maclean and Klinges 2021). Environmental data choices can substantially influence results. The ERA5 climate dataset (Hersbach et al. 2023) provides hourly estimates of a wide range of environmental variables, facilitating more precise microclimate modelling (Murphy 2000, Klinges et al. 2022, Man et al. 2023). Climate change projections must align with relevant spatial and temporal resolutions (Guisan et al. 2019). Beyond reporting data sources, we recommend specifying temporal and spatial resolution and rationale behind variables selection when constructing MNMs. Projections can yield critical information on likely species spread, habitat suitability, and inform management interventions, particularly for invasion hotspots, protected areas and range edges. Furthermore, comparing MNMs with correlative SDMs can enhance understanding by identifying non-environmentally driven occurrences (Vaughan and Ormerod 2005, Levine et al. 2009, Wilson 2011, Dormann et al. 2012, Huang et al. 2018, Higgins et al. 2020).
6) Limitations acknowledgement. All models are simplifications of reality, and we found that MNMs built for invasive species tend to focus on capturing only one or two key limiting process, which likely reflects the high data requirements of more complex models. A key step is thus to acknowledge potential limitations of the model. This should include processes that are not considered in the model (e.g. dispersal, habitat and prey availability), potential for intraspecific variation, the impact of spatial and temporal resolution of the environmental variables and their interactions, non-linear responses (hysteresis) and life stages considered, extreme events, memory and priming responses or stochasticity (Suárez-Seoane et al. 2017, Briscoe et al. 2019, 2023, Riddell et al. 2023). Sensitivity analysis can be used for unknown parameters and/or include trait variability into the model to account for uncertainty in model outputs (Mitchell et al. 2017, Strubbe et al. 2023). Rather than working towards a complete MNM model for an invasive species, it might be more effective to develop tailored MNMs that respond to specific management cases or environmental spaces as a first step, while advances in data collection and integration continue to progress.

Revisiting correlative SDMs limitations: when and how is an MNM appropriate?

MNMs provide detailed, process-driven insights into species' physiological responses, but may lack fine-scale temporal and spatial information, such as microhabitats, competition, and biotic interactions, which correlative SDMs often capture implicitly (Mathewson et al. 2017, Davis et al. 2024). MNMs excel at broad-scale predictions by linking species distributions to mechanisms like thermal tolerance, metabolic rates, or water balance (Kearney and Porter 2009). At the same time, if parameterised with fine-scale variables, MNMs are very useful at the range edges, where climate is limiting (Briscoe et al. 2016). However, essential spatiotemporal invasion complexities driven by human activities such as trade, transportation, urbanisation and land-use changes, and new biotic interactions in the invaded range are not easily modelled through frameworks that focus solely on physiological limitations. This section revisits when MNMs offer useful projections of invasive species under climate change.

The use of MNMs to overcome the limitations of SDMs for invasive species is challenging, especially when modelling large numbers of species (Adde et al. 2023) and data-poor species (Pang et al. 2024a). Still, MNMs have been used to predict potential ranges of 20 invasive birds in Europe (Strubbe et al. 2023), and to estimate heat stress risk for 5203 frog species (Pottier et al. 2025), the latter relying on a phylogenetically informed data-imputation approach to fill data gaps. However, to date, studies have found varying results when assessing the strength of phylogenetic signal in relevant physiological traits across different taxonomic groups (Lancaster and Humphreys 2020, Roeder et al. 2021). Similarly, trait-based model transferability may aid predictions for structurally similar species (Vesk et al. 2021, Medeiros et al. 2023). Overall, if parameterised accordingly, MNMs can overcome almost all correlative SDM limitations when predicting invasive species potential under novel climates, but are less suited for estimating invasion speed or reconstructing invasion history (Briscoe et al. 2019).

MNMs might fail when: 1) distribution limits of species are not limited by the environment but driven by availability of disturbed habitats; 2) species physiological performance depends strongly on environmental interactions (e.g. temperature and moisture) and these are not captured in the model; or 3) a model fails to capture the actual conditions to which the species is exposed, including inadequate temporal and spatial resolution. Parameterising MNMs can also be particularly challenging for 4) species with slow growth rates, long generation times, stage-specific physiological sensitivities or complex behavioural responses, but where feasible, MNMs that capture these complexities can be powerful (Benito Garzón et al. 2019). For 5) species expanding due to human activities (e.g. of commercial interest) or degraded habitats, occupancy dynamics and connectivity may outweigh the niche construction process and physiological constraints (Odling-Smee et al. 2003). Furthermore, 6) species with high interspecific and intrapopulation variability (e.g. morphological plasticity, genetic diversity) complicates experimental designs for MNM construction.

Conversely, MNM are likely to be better than correlative SDMs in predicting future distribution when: 1) species are in early stages of invasion and the invasive region has large areas of novel environments not captured in the native range, 2) biotic interactions are vastly different in the invaded range or are expected to change drastically with climate change, 3) genetic diversity in the invaded range complicates species identification, 4) species are commercially cultivated and naturalised, 5) time-lags drive expansion, 6) strong range-edge processes occur, and 7) multiple introductions create complex non-equilibrium distributions. In cases 3, 6 and 7, the MNM must be fitted with representative genotypes across the invaded range and/or at the range-edge. MNMs yield better predictions for species with detailed physiological data 8). Species with 9) high environmental sensitivity in early life stages integrate well into MNMs focused on the regeneration niche (e.g. requirements that sexually mature plants need to reach reproductive maturity, seed dispersal, germination, and seedling establishment; Grubb 1977), which is critical for invasive success (Guerra-Coss et al. 2021). Some taxa show stage-specific vulnerabilities (e.g. seed establishment in cliff plants; Aronne et al. 2023), whereas others experience life-cycle-wide sensitivities (butterflies' survival; Radchuk et al. 2013). Even pollen performance can be temperature-sensitive (Rosbakh et al. 2018), underscoring the challenge of integrating life-stage variability into MNMs. While focusing on key sensitive stages can make MNMs more tractable, more work is needed to identify key sensitive stages across different taxa and ecological contexts.

Mechanistic niche models and correlative SDMs are not entirely distinct approaches; rather, they lie on a spectrum of modelling complexity and process-explicit representation, ranging from models based solely on the fundamental to those relying only on observed species presence (Dormann et al. 2012). Hybrid models like CLIMEX fitted using occurrence data might circumvent data needs, but the capacity of those models to address certain research questions is limited by parameterisation. Models parameterised using species occurrence data may not provide useful predictions under novel conditions, especially during early invasion stages or when data are sparse (e.g. 19 of 50 top European invasive plants have < 500 GBIF records in the area, often linked to human presence). However, transferability remains possible in cases where the realised niche is conserved (Liu et al. 2022). Furthermore, recent advances in statistical approaches, including data pooling, downscaling or spatially-nested hierarchical models, allow the integration of models at the whole range scale (native and invaded range) with those at finer scales and higher resolution in restricted regional extents (invaded range) (Austin 2007, Guevara et al. 2018, Yates et al. 2018, Chevalier et al. 2021a, 2022, Goicolea et al. 2025). Additionally, strategies to minimise SDM biases due to distribution disequilibrium include data thinning, probabilistic models, multispecies approaches, and dispersal models (Sandel et al. 2025).

Despite their limitations, MNMs can produce a range of critical outputs for invasive species management. Those outputs typically do not include explicitly simulating population responses to a specific perturbation or management action or projecting invasion expansion rate through time, which might be better achieved with demographic distribution or individual-based models (Domisch et al. 2019, Briscoe et al.

2019). Nevertheless, outputs of MNM models can often be used to identify regions that likely fall outside the fundamental niche of the species, and to target invasive species control. For example, a MNM that predicted heat stress risk of feral cats in Australia based on simple assumptions about food intake was used to identify where access to rabbit burrows is likely to aid feral cat persistence – and thus where rabbit burrow removal could be a useful target for management (Briscoe et al. 2022). Similarly, MNM predictions of cane toad dispersal potential and survival under different environmental conditions informed a plan to close off access to water points in a region of Western Australia to prevent further spread (Tingley et al. 2013, Southwell et al. 2017). Also, for plants, capturing demographic dynamics of the garlic mustard in New England revealed that inhibiting spread into cold unoccupied areas is the most effective way to make population dynamics decline (Merow et al. 2017). More generally, the comparison of multiple insect invaders' potential distribution was used to assist management actions decision-making (Gutierrez and Ponti 2013).

Conclusions

Meaningful management decisions from SDMs require understanding the modelling decision process (Guisan et al. 2013, Schuwirth et al. 2019). Mechanistic niche models constitute an essential tool to link physiology with management needs by explicitly considering the drivers of species distributions (Evans et al. 2015). MNMs are particularly suited for predicting the potential distribution of invasive species as these organisms are often distributed across the landscape under non-equilibrium conditions that are difficult to model using correlative approaches.

Despite their potential, the application of MNMs to not only invasive but also other species remains limited due to substantial data requirements. Hybrid approaches, particularly those focused on invasive insects, dominate the field. The decisions made during MNM parameterisation – from genotype selection and fitting techniques for physiological models to projecting potential distributions – critically affect their accuracy and appropriateness for specific applications.

The ideal MNM design would incorporate biophysical models parameterised with data from laboratory experiments exposing representative genotypes to a wide range of environmental predictors. However, such designs demand expensive and time-consuming efforts, limiting their feasibility. Even the most robust MNMs built for invasive species lack some determinants of species survival. While MNMs that capture all key constraining mechanisms may be impossible – given that the necessary experimental data will probably never be available, as well as the context-dependent and spatiotemporal complexities of biological invasions (Laxton et al. 2023) – goal-oriented MNM for invasive species constitute better management tools than correlative SDMs to predict invasive species potential under climate change conditions at early invasion stages.

Integrating phylogenetic signals can reveal evolutionary constraints on species' responses to novel environments (Wiens et al. 2010), while trait-based approaches highlight the potential of functional traits to inform climatic niches (Medeiros et al. 2023). Cross-disciplinary collaboration – bridging physiology, physics, genetics, and ecology – can enhance the development of robust MNMs and standardise reporting practices, ultimately improving their reproducibility and broader applicability.

Finally, the insights gained from MNMs extend beyond invasive species modelling, offering valuable contributions to understanding climate-driven range shifts and guiding management actions for broader biodiversity conservation (Caplat et al. 2013, Wallingford et al. 2020).

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Erola Fenollosa: Conceptualization, Data curation, formal analysis, investigation, methodology, visualization, writing – original draft and feedback integration. **Roberto Salguero-Gómez**: Supervision. **Natalie J. Briscoe**: Methodology discussion. All authors (**EF**, **RS-G**, **Sean E. H. Pang**, **NJB**, **Antoine Guisan**) contributed to Writing – Review and editing, figure content discussion, and terminology revision.

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Supporting information

The Supporting information associated with this article is available with the online version.

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