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Powerful yet challenging: Mechanistic Niche Models for predicting invasive species potential distribution under climate change

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Abstract

Risk assessments of invasive species are among the most challenging applications of species distribution models (SDMs). This challenge arises from the disequilibrium in invasive distributions, where recorded occurrences do not fully represent the species' potential range. The spatiotemporal dynamics of invasive populations are shaped by intraspecific variability, human-mediated introductions, novel biotic interactions, climate change, and ecological niche shifts, which are only indirectly incorporated into correlative SDMs. Predicting future potential distributions under these conditions requires moving beyond traditional frameworks reliant on historical climatic data to models that explicitly capture the mechanisms underlying species potential. Mechanistic niche models (MNMs) address these limitations as process-explicit models that integrate species' physiological performance across environmental gradients. By incorporating physiological constraints and vital rates, MNMs define species distribution limits, offering a mechanistic understanding of species-environment relationships and enabling more robust predictions under changing conditions. However, a unified MNM framework remains elusive. In this review we delve into the theoretical foundations of MNMs, emphasizing their advantages over correlative approaches, especially for 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 revealed that MNMs have been applied sparingly to invasive species, focusing primarily on insects and plants, likely due to high data requirements. While MNMs do not explicitly capture spatial processes, they remain the most suitable approach for defining species distribution limits under novel conditions, but their success depends on the relevance of input data and effective parameterization, including genotype selection, model type, experimental conditions, and physiological curve-fitting techniques. MNMs offer significant potential for advancing ecological research and providing robust tools for evidence-based management decisions. By addressing key challenges, they can enhance our understanding of invasive species and other populations in disequilibrium under changing environmental conditions.

Keywords: Alien species, Biophysical, Ecophysiological niche models, Distribution forecast, 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). This topic 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).

Species Distribution Models (SDMs) are the most widely used tools for spatially explicit predictions of species' environmental suitability (Guisan et al. 2017) and have been extensively applied to explore invasive species' potential (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, including observation bias, the inability to capture non-equilibrium or source-sink dynamics, statistical extrapolation fallacies, and the lack of integration of species dispersal or biotic interactions (Lee-Yaw et al. 2022). Some of those limitations might be particularly relevant for invasive species, since they show non-equilibrium distributions because of incomplete range expansion, transient dynamics, or niche shifts from native and invaded ranges (Gallien et al. 2012; Elith et al. 2017). Biased observed occurrences challenge SDMs for all organisms (Dubos et al. 2022) but might be even more complex for species with rapid colonization speed like invasives (Gallien et al. 2012; Moudrý et al. 2024). Approaches such as pooling species, accounting for imperfect detection, and implementing autoregressive structures can help address spatial and sampling biases in species’ native range (Dorazio 2014; Fithian et al. 2015; Pacifici et al. 2017; Hui 2023; Soley-Guardia et al. 2024). However, mitigating bias for alien species in their invaded ranges is more complex, as additional mechanisms beyond heterogeneous sampling effort or imperfect detection are involved (as depicted in **Figure 1**, and exemplified in a specific case in **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 methods have been proposed. In this review we aim to (i) decompose the mechanisms behind biases or limitations that cause correlative SDM failure in invasive species, (ii) justify and define the foundations of mechanistic niche models (MNMs) and their potential for invasive species to solve correlative limitations. Specifically, MNMs (or ecophysiological models) aggregate process-explicit distribution models that explicitly test responses to specific environmental factors, approaching the species fundamental niche. Other process-explicit models such as demographic models, or abundancy dynamics will not be considered in this review, since they approach the realized niche, and thus they might fail to predict invasive species dynamics under changing conditions. While discussing these different mechanistic models, we will also (iii) explore how MNMs have been applied to project invasive species potential distributions and (iv) assess whether MNMs truly 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). Globalisation has facilitated the crossing of previously impenetrable geographic barriers, sometimes even transporting species in regions (i.e. geographic space) which climatic conditions are outside the species' native niche (i.e. environmental space). Transportation networks, trade, and international travel now serve as effective vectors for introducing non-native species (Westphal et al. 2008; Hulme et al. 2021; Gippet and Bertelsmeier 2021).

Historical empires have also left a legacy on global biodiversity. For instance, Lenzner et al. (2022) demonstrated how the colonial activities of four European empires—British, Spanish, Portuguese, and Dutch—structured current alien floras worldwide. Their study revealed that flora compositional similarity is higher than expected among regions previously under the same empire's influence. In one example, South African Aizoaceae plants, long cultivated in British gardens, likely facilitated the invasion of species such as hottentot-fig (*Carpobrotus edulis*), baby sun rose (*Aptenia cordifolia*), and pink ice plant (*Drosanthemum floribundum*) in Europe (Preston 1988; Campoy et al. 2018).

In addition to global trade, increased propagule pressure might allow urbanised areas to temporally sustain invaders. Urbanisation is a major driver of exotic species richness (Heringer et al. 2022). Disturbed communities often host lower biodiversity and have been described as less resistant to invasions, although this relationship may vary with the invasion stage (Stachowicz and Tilman 2005; Guo et al. 2024). Lower biotic resistance and increased resource availability in disturbed environments explain the presence of the bermuda buttercup (*Oxalis pes-caprae*) in its invaded range (González-Moreno et al. 2015).

Highly populated areas are subject to higher invasive propagule pressure due to global trade, which increases the likelihood of successful establishment (Borden and Flory 2021). For example, the pinewood nematode (*Bursaphelenchus xylophilus*) in China is more likely to occur in areas with high human population density (Robinet et al. 2009). Connectivity, such as road networks, further facilitates human-mediated species distribution by amplifying plant invasions and enabling dispersion in disturbed habitats (Son et al. 2024). Connectivity not only enhances range expansion but also the likelihood of species detection. Spatial autocorrelation in species records (not only at the invaded range) often reflects uneven sampling efforts and site accessibility (e.g. roads, urban areas; Dormann et al. 2007; Botella et al. 2020). An interesting case involves the invasive bluegill (*Lepomis macrochirus*), where the fish's presence in ponds correlates with the visibility of those ponds from nearby roads. Increased visibility attracts fishing activities, a key introduction pathway for this species (Kizuka et al. 2014).

Even though connectivity might explain the arrival of a species in a specific location, it does not guarantee species success. Approximately 40% of global invasive species were intentionally introduced for their charismatic appeal or specific functional uses, such as terrain stabilisation, fishery support, or culinary purposes (Turbelin et al. 2017). These intentional introductions often occurred outside the species' native climatic niches. Human activity has been found to drive the establishment of non-native plants on islands, but not their subsequent invasion (Pfadenhauer et al. 2024). Records in citizen science platforms such as iNaturalist may fail to indicate whether observations represent casual or wild populations (López-Guillén et al. 2024), impacting correlative SDM predictions. Similarly, Hui (2023) highlights that occurrence records often lack details on whether they represent established or sink populations, which would pose distinctive expansion risk. Consequently, invasive occurrences are strongly influenced by the impact of human activities and movement.

Overall, urban and disturbed areas exhibit increased alien species richness due to heightened propagule pressure, reduced biotic resistance, and increased resource availability. Whereas using the native range occurrences to capture species presence in the invaded range might fail due to underestimation around urbanized areas, using the invaded range occurrences to predict future distribution might fail as well since occurrences do not constitute established populations. The usage of both native and invaded ranges registers has been proposed (Broennimann and Guisan 2008) but this approach might require niche conservatism, which will be discussed in the next section.

Niche shifts: Invasive species might grow in conditions outside their native niche

After arriving in a novel environment, one of the primary factors determining a species' establishment is habitat suitability (Weiher and Keddy 1995). Habitat suitability depends on the climate, resource availability, and the presence of native competitors or predators (Hirzel and Le Lay 2008). Invasive species often thrive in environments resembling their native habitats but with fewer natural enemies, allowing rapid spread—a concept known as the Enemy Release Hypothesis (Keane and Crawley 2002). For example, invasive mammals are more likely to establish when introduction sites fall within their native climatic niche (Broennimann et al. 2021). However, invasive species can also experience shifts of their niche during invasion (Guisan et al. 2014), in which case fitting the SDMs with data from both the native and invaded ranges could capture better the current species distribution (Broennimann and Guisan 2008; Kearney et al. 2010).

When contrasting realised niches from invaded and native ranges, studies with plants generally support niche conservatism (Petitpierre et al. 2012; Liu et al. 2020a). However, while arriving in conditions belonging to the realized native niche may facilitate initial establishment, it does not guarantee invasive success (Broennimann et al. 2007; Divíšek et al. 2018). This discrepancy might be due to (i) evolutionary processes that lead to a differentiation of the fundamental niche during the invasion process and/or (ii) even though the fundamental niche is conserved, only a subset of it was occupied in the native range (due to habitat availability or biotic interactions) (Broennimann et al. 2007; Qiao et al. 2017). This second case falls within the niche variation hypothesis, that suggests that populations released from competition (i.e. natural enemies for invaders), are able to expand their realised niche (Van valen 1965, Bolnick et al. 2007) For example, island endemics such as amphibians and reptiles demonstrate high potential to expand their realised niches, illustrating how environmental matching (i.e. matching conditions from occurrences between native and invaded range) is not always required for invasion (Liu et al. 2020b; Stroud 2020). Diverging metrics for niche contrasts accounting for habitat availability have hindered conclusive evidence regarding niche conservatism in invasive species (Bates and Bertelsmeier 2021).

Beyond habitat availability, evolutionary processes can explain invasive species success outside the abiotic conditions observed in the native range (Broennimann et al. 2007; Pearman et al. 2008). Rapid adaptation associated with the lack of natural enemies, founder effect and/or genetic drifts (Eckert et al. 1996), plays a critical role in invasive success, potentially leading to niche evolution (Pearman et al. 2008; Colautti and Barrett 2013; Fenollosa and Munné-Bosch 2019a; Campoy et al. 2021). For example, differential thermal sensitivity (i.e. fundamental niche shift) was reported between individuals from the native and invaded ranges in the hottentot-fig under controlled conditions (*Carpobrotus edulis*, **Box 1**). In such cases, using occurrences from the native range to fit SDMs is discouraged. For example, for the Asian yellow-legged hornet (*Vespa velutina nigrithorax*), correlative SDMs performed better when native distribution data were excluded (Barbet-Massin et al. 2018). Mixed results were observed for invasive beetles, with two of five species showing niche conservatism (Duncan et al. 2009), while cane toads (*Rhinella marina*) demonstrated a realised niche shift (Tingley et al. 2014).

Overall, whereas environmental matching might contribute to species establishment into novel regions, native occurrences do not always explain species potential growth on the invaded range. Native realised niche unfilling due to habitat or dispersal limitation and biotic interactions, as well as fundamental niche shifts due to genetic bottlenecks and/or rapid adaptative processes in response to enemy release and/or founder effects, explain this climatic mismatch. Selecting the proper data for fitting SDMs (only native, only invaded, both or specific subsets of occurrences) would require a full characterization of those processes, which is not usually available.

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

Time plays a complex and non-linear role in defining the distribution of invasive species (Broennimann et al. 2014; Theoharides and Dukes 2007; 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, with annual self-fertilising or non-sexual reproduction species being less likely to experience prolonged lags (Robeck et al. 2024). Once established, the spatial spread of an invasive species is often determined by local environmental conditions and reproductive strategies. Species with high fecundity and adaptability tend to colonise new areas more rapidly (Capellini et al. 2015; Allen et al. 2017). A recent meta-analysis found that invasive plants' population growth rates increase with residence time, highlighting how these vital rate changes can complicate predictions of species potential (Suárez-Seoane et al. 2017; Gruntman and Segev 2024).

Climate shifts, land-use changes, management actions or resource availability can trigger sudden outbreaks, accelerating the spatial and temporal spread of invasive species. These shifts can lead to rapid, unpredictable changes in distribution patterns. In the case of the spotted knapweed (*Centaurea stoebe*), its invasion followed an initial spread phase in ruderal habitats, and a niche expansion into climates not occupied in the native range was observed after an extended lag phase (Broennimann et al. 2014). Additionally, conservation actions—such as mitigation efforts or habitat restoration—can further influence invasion dynamics, although these are often underrepresented in distribution models (Pyšek and Richardson 2010). SDMs fitted at different scales can be strongly informative to design management actions and monitor invasion potential, as done with the giant hogweed (*Heracleum mantegazzianum*) in Switzerland (Shackleton et al. 2020). Overall, registered occurrences at a given time often fail to capture the full potential of invasive species, as they are shaped by establishment lags, adaptive processes, and management interventions as well as by the complex source-sink dynamics discussed previously.

Populations within the invaded range may have different potential distributions. High intraspecific variability within invaded ranges due to multiple introductions, along with hybridisation and rapid adaptation, can result in population differentiation within a single species' invaded range, potentially leading to niche differentiation (Pearman et al. 2008; Pearman et al. 2010; Colautti and Barrett 2013). For example, local adaptation in purple loosestrife *(Lythrum salicaria)* was observed along a 1000-kilometer climatic gradient in the invaded range (Colautti and Barrett 2013). Rapid adaptation during range expansion may lead to genetically distinct populations, as demonstrated by wolves (*Canis lupus*) in Central Europe (Szewczyk et al. 2019). SDMs calibrated with occurrences from both confirmed and unconfirmed populations of the invasive turtle pond slider (*Trachemys scripta*) revealed contrasting projections, emphasising its strong expansion potential (Cordier et al. 2020). SDM calibration with naturalised populations outperformed SDMs calibrated using combined native and invasive records of common ragweed (*Ambrosia artemisiifolia*) (Dullinger et al. 2009). Similarly, models calibrated with early invasion data may underperform compared to those using established populations (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. We propose coining this phenomenon as “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, with extensive documentation in China (Ni and Hulme 2021), Indonesia (Junaedi et al. 2021), and Europe (Klonner et al. 2019). Urban trees planted outside their native niches also exhibit wider realised niches than native species (Kendal et al. 2018). Economic interests, such as the ornamental trade, contribute to this process, as seen with sacred bamboo (*Nandina domestica*) in the USA (Beaury et al. 2021; Bradley et al. 2022).

Populations at the edges of a species’ range—where physiological stress, 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). The centre-periphery hypothesis posits that demographic performance declines from the centre of a species' range towards its edges, potentially overestimating distribution when edge populations are treated as established ones. While this hypothesis has been supported in marginal climates (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; Csergö et al. 2017; Pironon et al. 2017; Angert et al. 2020; Chevalier et al. 2021; Kunstler et al. 2021). Interestingly, probably due to the expansion dynamics, invasive plants often exhibit higher growth rates in edge populations compared to central populations (Gruntman and Segev 2024).

Despite its critical importance, intraspecific variability (including population’s variability within species range) remains underrepresented in distribution models (Pearman et al. 2010; Collart et al. 2021). The high sampling effort required to capture this variability and the absence of established frameworks to integrate it pose significant barriers (Collart et al. 2021; Song and Li 2023). This gap in modelling limits the ability to accurately predict distributions for species with variable populations, particularly those undergoing rapid expansion or adaptation in their invaded ranges.

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

Identification challenges are a general limitation of correlative SDMs as they depend on occurrence data. Small, camouflaged, elusive, or subterranean species pose additional barriers to accurate monitoring (Jarić et al. 2019; Richter et al. 2021). However, these challenges are exacerbated in invasive species. Hybridisation, strong genetic admixture, or genetic bottlenecks because of the fast adaptation processes at novel environmental conditions might hinder a clear identification, leading to incomplete or inaccurate occurrence records.

Crypticity in species identity in its invaded range (Jarić et al. 2019) or during range expansion (Rosche et al. 2024) represent a significant source of observational bias, deeply affecting the outputs of correlative SDMs. While citizen science platforms such as iNaturalist provide valuable insights into invasive species distribution, the quality of data—particularly proper species identification—requires careful consideration (López-Guillen et al. 2024).

Fast adaptations, genetic admixture, and hybridisation during invasive expansion can lead to significant genetic and morphological complexities, making species identification challenging, particularly in plants. Examples include the native-invasive admixture of common reed (*Phragmites australis*) (Pyšek et al. 2018), genetic clusters of hottentot-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. 2024), the enigmatic complex of lantana (*Lantana camara*) (Goyal et al. 2015), and confusion between devil's backbone (*Kalanchoe daigremontiana*) and its invasive hybrid *K.* × *houghtonii* (Herrando-Moraira et al. 2020). Taxonomic uncertainty can also hinder invasive species monitoring, as seen with peppermint shrimp (*Lysmata vittata*), where conflicting morphological descriptions, inconsistent terminology, and limited molecular data complicate identification (Aguilar et al. 2022).

Predicting to novel conditions requires a full understanding of species' physiological limitations

Different climatic scenarios can significantly alter species’ potential for persistence and colonisation (Pironon et al. 2017). This necessitates training models not only with past and current environmental conditions but also with information on species' ability to face novel conditions (Kearney and Porter 2009) including extreme climatic events (Perez-Navarro et al. 2022). Incorporating such data is critical for predicting species distributions under climate change scenarios.

Novel environmental conditions can result from environmental drivers falling out of the explored ranges, or because novel combinations arise (Elith 2017). Climatic or bioclimatic variables of known species locations are the predominant predictors used in invasive SDMs, often supplemented with topographic, pedological, and anthropogenic variables (López-Tirado and Gonzalez-Andújar 2023). However, novel climatic conditions, which by definition have not been observed, require the understanding of the species’ fundamental niche to make accurate predictions (Kearney et al. 2009; Elith 2017; Briscoe et al. 2023).

Correlative SDMs assume that abundance reflect species physiological limitations, which are homogeneous within the species range. However, physiological plasticity is a complex trait susceptible to local adaptation (Fenollosa and Munné-Bosch 2019b). Lower temperature physiological limits are not constant across the invaded range of the cane toad (Kolbe et al. 2010), as it isn't some woody species drought tolerance to extreme events (Perez-Navarro et al. 2022). Such dynamics remain unaddressed in correlative SDMs that rely on past and present conditions on registered presences to define species physiological limits, which limits their predictive accuracy to under changing climates.

Invasive species spatio-temporal complexities as an adaptation laboratory

The distribution of invasive species is uniquely shaped across space and time (Laxton et al. 2022, **Figure 1, Box 1**). Since the species distribution on the invaded range is in equilibrium with their environment, their distributions and impacts are affected by factors beyond abiotic conditions and are changing at relatively fast rates (Werner et al. 2024). Alternatives to correlative SDMs offer promising approaches to capturing these complexities, especially under climate change scenarios. This is crucial not only for addressing the biodiversity threats posed by invasive species but also for advancing our understanding of ecological adaptation over relatively short time-periods.

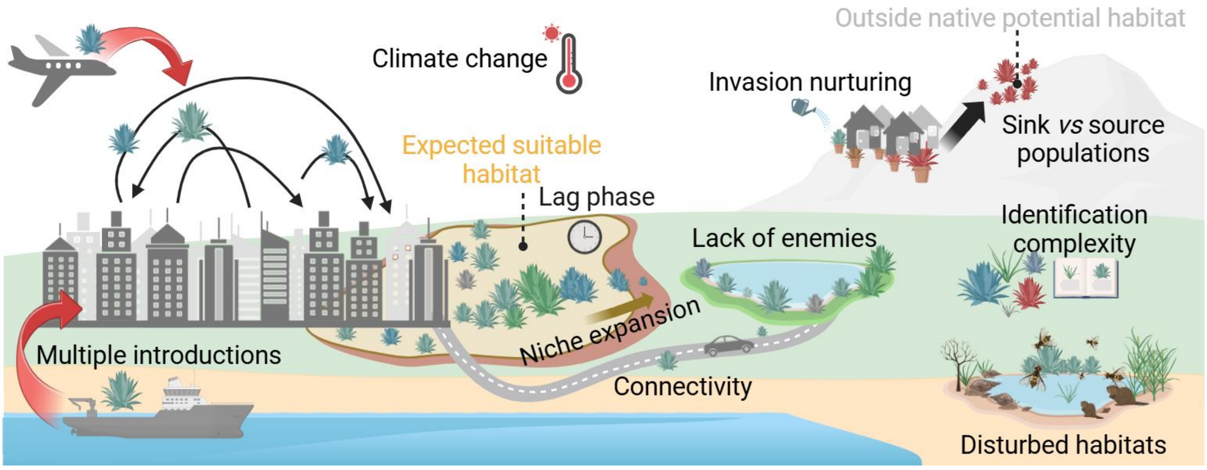


Figure 1. **Schematic representation of spatio-temporal complexities of invasive species distributions, from their arrival to their expansion**. Multiple introductions increase propagule pressure and facilitates invasions. Some species might not occupy all potential climatic niche due to lag phase and might shift with climate change. Connectivity to disturbed habitats and without natural enemies of the introduced species might facilitate and accelerate invasive spread. Invasion nurturing facilitates climate discovery to novel areas. Not all occurrences might constitute stablished or source populations. Identification complexities might hinder invasive species registrations. For further details, refer to the text. Created with BioRender.

BOX 1. Spatio-temporal complexities of an invaders case study, the hottentot-fig invasion.

The invasive hottentot-fig (*Carpobrotus edulis*) is a succulent clonal plant native to the Cape region of South Africa. Its reptant stems form dense mats, enabling it to thrive in diverse environments (Wisura and Glen 1993). The species 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 that exposed mechanistic determinants behind *C. edulis* success that limit the predictive capacity of correlative SDM as a case example (**Numbered in Figure 2**). (**1)** Ornamental interest increases propagule pressure both within and outside its suitable range. For instance, in its native range, the species experiences annual rainfall of 464 mm but invades areas like Galicia (NW Spain), which receive 1228 mm (Picture: E. Fenollosa). (**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 (Pictures from Campoy et al. 2021 and Fenollosa and Munné-Bosch 2019a). (**5**) Realised niche shift towards colder regions was found between European (invasive) 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**) CAM shift and 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 spatio-temporal complexities of invasion, demonstrating the limitations of correlative SDMs and emphasising the importance of mechanistic approaches.

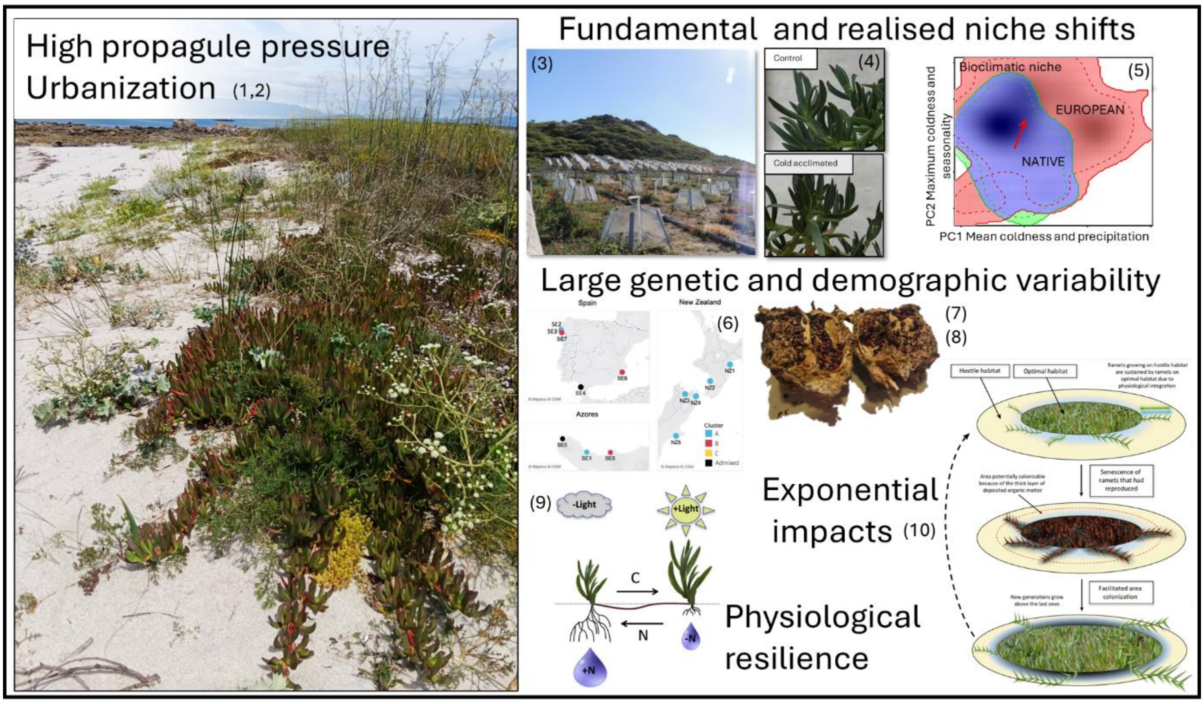


Figure 2. Ten studies compendia with the invasive hottentot-fig (*Carpobrotus edulis)* via mechanistic lens, highlighting the elements that shape its distribution, hindering accurate forecasts using correlative SDMs. Pictures credit is acknowledged in Box 1.

Mechanistic Niche Models: forecasting species potential from physiological limitations

Given that correlative SDMs may be unreliable for species with non-equilibrium distributions (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. In response, ecologists are increasingly incorporating biological processes into distribution predictions.

There are a range of process-explicit models that explicitly account for processes such as physiology, dispersal, demography evolution and biotic interactions (Briscoe et al. 2019; 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 variously referred to as eco-physiological 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) hereafter but highlight the implications and potential challenges of differences in parameterisation.

We focus on MNMs because 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 traits (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.

While MNMs share some similarities with process-explicit models that also aim to capture demographic responses to environments (i.e. demographic distribution models; Merow et al. 2017), we differentiate them here by emphasizing their mechanistic basis in physiological processes and constrains as a function of environmental variables, as opposed to relying primarily on demographic patterns from field data or modelling individual's physiological processes without considering environmental influence.

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 species distribution models (SDMs) (e.g. Schwinning and Parsons 1996; Kearney and Porter 2009), and the need for combined expertise in modelling, demography, and environmental physiology has hindered the widespread adoption of MNMs (e.g. Buckley et al. 2010; Kearney et al. 2012; Woodin et al. 2013). Kearney and Porter (2009) identified a major barrier 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 rooted in ectotherm studies (Tracy 1982) 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 (recently reviewed by Ridell et al. 2023). Biophysical models have mainly been used in ectotherms, though their use in endotherms is growing (Angilletta 2009; Briscoe et al. 2023; Ridell et al. 2023). Similarly, dynamic energy budget (DEB) models, which can be integrated within biophysical ecology (Kearney et al. 2010), have been also 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, species survival is often possible over a wider range of temperatures than locomotion or reproduction (Buckley and Kingsolver 2012). Overall, data requirements for MNMs vary significantly depending on the organism type, as different species demand unique physiological, demographic, or environmental datasets to accurately represent their responses to ecological conditions.

While MNMs have primarily focused on environmental variables such as temperature, other key mechanistic elements that shape species distributions could also be incorporated. Although temperature significantly influences species performance, species-specific critical temperatures often fail to fully explain biogeographical patterns (Sunday et al. 2012), mainly because they are often not solely or directly related to range limits and need to be integrated with other parameters in biophysical models (Chevalier et al. 2024). 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).

Mechanistic niche models mark a significant advancement in ecological modelling by linking physiological processes with species distributions to deliver biologically grounded predictions. Unlike correlative SDMs, MNMs explicitly incorporate physiological and demographic data, 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, e.g. Adde et al. 2024), these models 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

Mechanistic niche models have emerged as a powerful tool for understanding the environmental and biological constraints shaping the distribution of species (Kearney and Porter 2009; Evans et al. 2015; Briscoe et al. 2019). 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 parametrize the model, we performed a systematic review of published studies using MNMs in invasive species worldwide (**Supplementary material 1**). Briefly, we based our search on Briscoe et al. 2019 search terms to obtain three types of models: MNMs, demographic distribution models (DDMs) and individual-based models (IBMs), combined with filters to detect studies with invasive species. Although demographic distribution and individual-based models were out of the scope, we included them in the search terms to check if some of them could be also 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 (and not field data, as discussed in the previous section).

Mechanistic niche models have been used to a very limited extent. Our systematic review resulted in 53 articles including MNMs for invasive species from 2007 to 2024 (**Figure 3**). 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 to name these models across studies further complicates their application. 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 et al. 2012), biologically informed (Lozier and Mills 2011), biophysical (Tingley et al. 2014), temperature-driven (Logan et al. 2007), ecophysiological (Ginal et al. 2021), process-based (Gutierrez et al. 2007), 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 rather rare. Instead, researchers have been attempting to include some key processes or physiological constrains, and in some cases use pre-built frameworks or transferring physiological data from other species. Since some of those pre-built frameworks can include some data from species occurrences, when they do, they do not constitute mechanistic but hybrid approaches. Some examples of these pre-built frameworks (some of them could be mechanistic, or hybrid depending on the data use to parametrize it) are the CLIMEX model mainly used for insects (e.g. Ponti and Gutierrez 2023), the TTR (Thornley transport resistance) (Higgins and Richardson 2014; Higgins et al. 2020) or dynamic vegetation models such as LPJ-GUESS for plants (Leiblein 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). Considering the strong data requirements for a fully mechanistic approach, we decided to include and discuss benefits and limitations of all those approaches, which in some cases will not be suited to understand invasive species potential distribution under novel environmental conditions. When classifying the studies in our review by MNM modelled taxonomic groups, over 50% focused on insects while nearly 20% addressed plants (**Figure 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 ecological impact and ability to rapidly colonise new environments. The extensive usage of MNMs in insects responds mainly to these species' strong dependence on temperature as well as their potential to act as vectors for disease (Rebaudo and Rabhi 2018). Besides insects and plants, four articles reported MNMs with amphibians, microorganisms (virus, Taylor et al. 2019), 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) (**Figure 3, Supplementary Material 2**).

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, some of these studies aim 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 (**Figure 3)**. To do so, authors built both correlative models and MNMs and contrasted the resultant projections sometimes considering variables of interest. One of the examples of this application is the study of the sub-Antarctic insect by Pertierra et al. (2020). In this work, a MNM was parametrized from vital rates as function of temperature obtained after laboratory experiments where survival, growth and fecundity were monitored in larvae exposed to 0, 2, 4, 6 and 8ºC for 30 days simulating the austral summer. The contrast of this MNM to a correlative SDM revealed high potential for the species to expand their invaded range and exposed how its current distribution is shaped by human presence.

Other applications of MNM in invasive species included: comparing multiple invaders' potential distribution to assist management actions decision-making (Gutierrez and Ponti 2013), test niche conservatism or niche shifts between invaded and native ranges (Tingley et al. 2014) and understand the role of intraspecific variability in species distributions (Kolbe et al. 2010). In some cases, both native and invasive species distributions were parameterized, such as the pathogen Bsal (*Batrachochytrium salamandrivorans)* with the threatened native fire Salamandra (*Salamandra salamandra)* to determine extinction risk (Deiß et al. 2024). In addition, some articles also used MNMs to predict invasion dynamics, but to do so, mechanistic models were coupled with occupancy data to predict spread. This is the case of the study by Walter et al. (2023), where the temperature-dependent developmental performance of the spongy moth (*Lymantria dispar dispar*) was used 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. Other studies predicted invasion spread from physiological data by parametrizing the model with time-dependant rates (Hartley et al. 2010). In this study by 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, resulting into a rate-of-spread, and predicting future range expansion.

Our review identified several approaches used to meet data requirements for constructing MNMs. Thermal tolerance was the most frequently used variable to build response curves for invasive MNMs (e.g. 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 parametrize MNMs. Some examples include modelling the timing of the breeding season with 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 has been the most selected trait in the reviewed studies, other traits, such as reproductive components or specific metabolites levels have also been incorporated 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), others were built from laboratory tests conducted under a limited number of experimental conditions (e.g. five different temperatures) or combined both via energy-mass balance equations. All modelling approaches result in a model where a performance variable is a function of the 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 the 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 produce a continuous thermal curve, they require extensive species-specific knowledge. For instance, Kearney et al. (2008) incorporated numerous parameters for amphibians, including equations for heat exchange via cutaneous evaporation, surface-body mass functions, the distance of an average adult from the ground, active posture surface fraction, postural change effects, nocturnal activity regimes, relationships between body temperature and water loss, movement capacity and frequency at different temperatures, feeding rates, annual water balance, metabolic rate and body temperature relationships, cutaneous and respiratory water loss rates, water excretion, lethal temperatures for eggs and larvae, egg development rates at different temperatures, and sensitivity to pond configurations.

Individual’s representativity must be considered when building MNMs, since it might limit our ability to capture invasive species’ non-equilibrium dynamics. Kolbe et al. (2010) showed that low temperature tolerance is not a constant trait across the invaded range of the cane toad, and therefore, just a sampling site to collect individuals would not represent the potential expansion of the species. For this reason, 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 using 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 on the use of physiological thermal limits obtained from physiological experiments to capture the species distribution limits, particularly at lower temperatures, since adaptive and/or facilitative mechanisms could allow species to survive in temperatures below physiological limits (Chevalier et al. 2024). Unlike direct methods, inverse data collection (from individuals occurring in areas with differentiated environmental conditions) can capture environmental complexity beyond fixed temperature regimes (Evans et al. 2016). Latitudinal, altitudinal, or moisture gradients have been employed to parameterise some parts of MNMs for invasive species (Augustinus et al. 2020; Pasquali et al. 2020). However, it is crucial to note that inverse methods model the realised niche rather than the fundamental niche. Given that the realised niche of invasive species may not fully represent their potential range, projections based on such models may be biased, limiting their reliability for predicting future distributions.

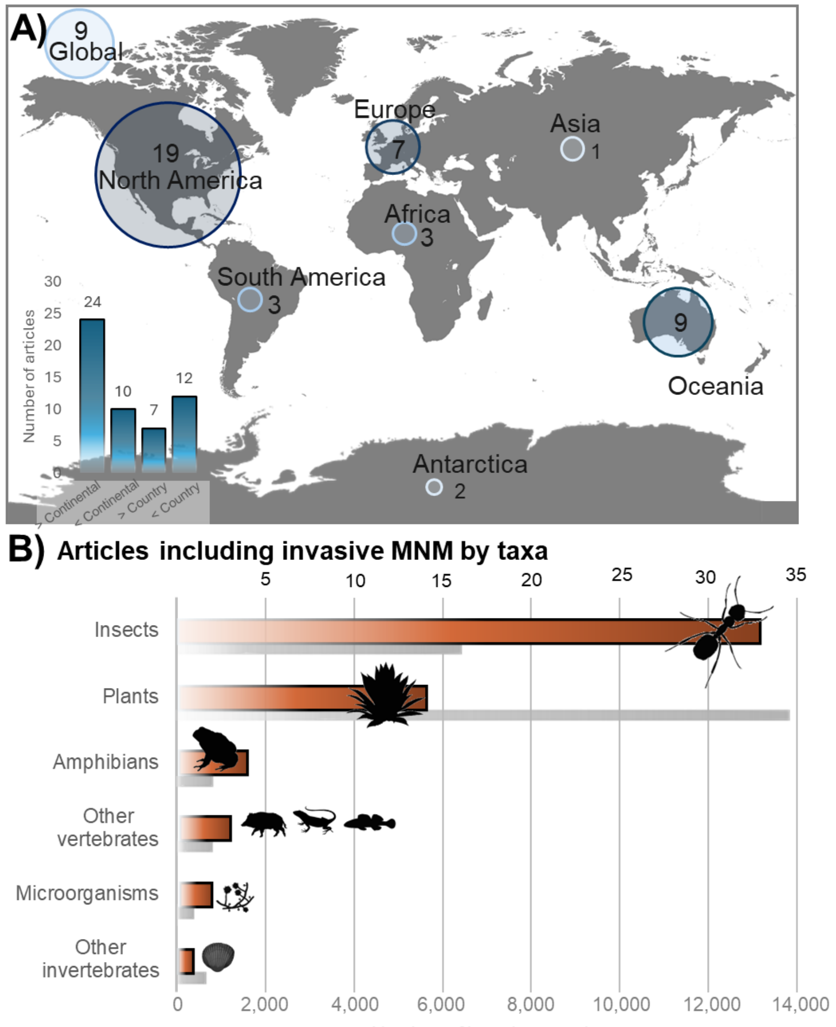
Another used method to integrate more environmental conditions rather than a single environmental variable is the one taken by Merow et al. (2017), who modelled the invasive garlic mustard (*Alliaria petiolata*) and Japanese barberry (*Berberis thunbergii*) by collecting demographic data from an experimental setup including a series of transplant plots across diverse environments within the invaded range. However, categorising this approach as a MNM is delicate, as the model was defined as a demographic distribution model, but data from experimentation (not under fully natural conditions) was used to explore physiological responses to the environment. More importantly, the capacity of these type of models to capture invasive species fundamental niche to project their potential to novel conditions is strongly limited by the fact that non-novel conditions are explored. Experimental design and data parametrization must be wisely 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), sometimes based on pre-built frameworks. Depending on how these models are parameterised, they may either inherit the limitations of correlative SDMs or align more closely with MNMs by incorporating non-environmental drivers, but the limit will be difficult to assess in most cases (Chevalier et al. 2024). 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) and 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 other pre-build mechanistic frameworks, reaction norms in response to environmental factors can be fitted with experimental data but also with species occurrences, and only the first case will be a mechanistic approach (Ponti and Gutierrez 2023).

Some studies using the CLIMEX framework derived species physiological limits from native versus invasive occurrence data (Shabani and Kumar 2015). While this approach accounts for realised niche shifts between native and invaded ranges, it remains constrained by reliance on registered occurrences, which may not fully capture the species' potential range. For example, the usage of previously described thermal curves (e.g. Walter et al. 2023) from populations from the native range might not represent the invasive individuals. Recently, Formoso-Freire et al. (2023) demonstrated how a hybrid model combining an MNM with a correlative SDM for the invasive Asian hornet (*Vespa velutina*) provided insights into both the temporal dynamics of range expansion and long-term potential distributions. Since hybrid models also allow the inclusion of dispersal aspects in invasive species (Robinet et al. 2009; Klonner et al. 2019) the authors suggest are appropriated when aiming to model invasion rates under global change, particularly in data-limited contexts (Rodríguez et al. 2019; Bosch-Belmar et al. 2021; Guillaumot et al. 2022; Tourinho et al. 2023). However, considering the recent work by Chevalier et al. (2024) we are critical with combining physiological thermal limits with species presence, especially for invasive species with non-equilibrium distributions and complex spatio-temporal dynamics. These critical physiological measures need to be instead integrated, together with other parameters, in a mechanistic model.

Beyond CLIMEX, other pre-built frameworks being used for invasive species fall within a subset of MNMs that integrates species' thermodynamical relationships with their environment and includes): TTR (Higgins et al. 2020), or LPJ-GUESS (Leiblein-Wild et al. 2016). These models focus on simulating energy, resource transport, and physiological processes to estimate species performance and potential growth. TTR models simulate the transport of nutrients, water, and other resources and tend to focus on quantifying the resistance to transport between tissues and ultimately estimate individual's potential growth (Higgins and Richardson 2014; Higgins et al. 2020). Similarly, NicheMapper is based on energy balance equations and are mainly applied to endotherms and ectotherms (Kearney and Porter 2019; Briscoe et al. 2023). These biophysical models have been used mainly on invasive amphibians, and they use detailed physiological parameters such as metabolic rates and survival, development or growth in response to temperature, given these taxa strong dependence on temperature. Other 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. Consistent with findings from other systematic reviews on correlative SDMs (Lantscher et al. 2018; López-Tirado and Gonzalez-Andújar 2023), North America accounted for the highest number of invasive species MNM studies (**Figure 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 or experimental installations, 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.



C) Applications

- ○ Climate change projection (included by 47.2% of studies) [16]
- ○ Compare invasive species to prioritize [2]
- ○ Test the contribution of environmental vs non-environmental drivers to species distribution [13]
- ○ Understand the role of intraspecific variability in species distribution [2]
- ○ Test niche conservatism and unfilling [7]
- ○ (*)Predict invasion dynamics [3]

(*) Not only MNMs

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 colour 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 predominant protagonists in 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. Under brackets, the number of articles.

A unified framework for invasive mechanistic niche modelling

Despite several articles covering the do's and don'ts, key aspects to consider, top hazards, and step-by-step guides for correlative SDMs (for recent articles see e.g. Araújo et al. 2019; Zurell et al. 2020; Sillero et al. 2021; Hui 2023; Soley-Guardia et al. 2024; Davis et al. 2024), a framework for designing, building, and reporting MNMs in invasive species is still missing (but see Kearney and Enriquez-Urzelai (2023) framework for developing eggs mechanistic modelling, Ridell et al. (2023) review on biophysical models, Da Re et al. (2022) unified modelling framework for invasive *Aedes* mosquitos and Buchadas et al. (2017) review on dynamic models for invasive species management). We propose here the following steps when building an MNM for determining the potential distribution of invasive species, schematized in **Figure 4**.

1) Research aim. Given the importance of the research aims on the parameterization of the MNM, the first step when building an invasive MNM is to delimit the ecological question, management goal, or knowledge gap that we intend to address. As discussed in the previous section, MNMs are adequate for determining the potential for expansion of an invasive species toward higher latitudes, estimating distribution shifts with climate change, quantifying the niche overlap with threatened species, or potential biocontrol agents, test the contribution of environmental versus non-environmental distribution drivers or detect niche unfilling (**Figure 3**). The research aim will allow us to distinguish if we should look for upper thermal limits (in case we want to assess niche shifts towards warmer climates; but see Chevalier et al. 2024), quantify vital rates (if we aim to find species reproductive limits) or to prepare an experimental design with competition and density-dependence (in case we want to model species competition with climate change). In biophysical models, multiple complexity levels can be included. For example, we can aim to model the heat budget of a single life stage, multiple life stages, include activity or not only include temperature balances but also water and food for instance (Briscoe et al. 2023). Finally, the spatio-temporal complexity associated with the invasion process must be gathered (**Figure 1**). These key aspects include the overlap between niches obtained from native and invaded occurrences, if the species has ornamental interest that could led to invasion nurturing, if it has commercial interest that could lead to increased propagule pressure in highly connected areas, if there are any identification complexities, and the time since introduction. The choices made at this stage will shape the outcomes of the MNM, making it essential to align model complexity and data requirements with the research aim.

2) Genetic integrity. Prior to building a physiological model the species material must be selected according to the research aims, the degree and importance of the described genetic variability and considering the invasion dynamics literature. In **Figure 4** we depicted four species material selection strategies for MNMs used in the reviewed literature. However, some of them might limit our capacity to overcome correlative SDMs limitations for invasive species, and thus, must be carefully selected. For example, Kolbe et al. (2010) showed that individuals from different populations of the cane toad within the invaded range had differential low-temperature tolerances. To capture such intraspecific variability, it is required to sample multiple populations from the invaded range representing the climatic and geographic niches (Gallien et al. 2012). Other alternatives, such as using a single population, can be considered in case low variability across populations has been described for this species for the selected trait, or to use data from the native range only if we know the trait is maintained between native and invaded ranges. Sensitivity analysis can assist delimiting the importance of intra or inter-population variability over certain traits. One approach to include trait variation is the one taken by Strubbe et al. (2023), who first built species-level model for several bird species. The species-level model was subjected to a sensitivity analysis uncovering the most influential variables, which were used to build a and an intraspecific-level model accounting for trait variation. However, it must be noted that fitting a physiological model from a single population will not allow capturing range-edge processes. In all cases we encourage reporting the niche margin index (NMI) described by Broennimann et al. (2021), which reflects the relative distance of a population inside or outside the niche after estimating it and can also be used in a climate change context (Pearman et al. 2024). Since closely related species are likely to possess similar niche requirements (Wiens et al. 2009; Crisp and Cook 2012) a final alternative would be to use data from similar species could be a way to address data scarcity (James et al. 2021). In addition to species origin, we must consider life stage that we will be considering for our physiological model. Larvae are commonly used in insects' models given their sensitivity to climate change (Kingsolver and Buckley 2020).

3) Environmental drivers and response variables. MNM building requires the selection of environmental driver(s) and response variables as well as the delimitation of the relevant interval (e.g. temperature from 0 to 10°C) including the forecasted increase or decrease under climate change scenarios (e.g. +2ºC in mean temperature). Environmental drivers can include abiotic factors (Temperature, humidity, soil moisture, and atmospheric CO_2) and biotic factors (predators, competitors, host species, and symbionts). Environmental drivers' selection must follow an understanding of the abiotic and biotic factors that limit species survival, growth, and reproduction, and the spatial resolution at which they should be used (Spence and Tingley 2020), but these may strongly differ depending on the organism type. In case a biophysical model is used, which is often a preferred choice for endotherms, ectotherms and plants, a first step will be to design and decompose the model. Recent reviews by Riddell et al. (2023) and Briscoe et al. (2023) present multiple approaches taken for this crucial step. Interactions between environmental variables (e.g. moisture and temperature) frequently occur and should be considered when designing experiments to measure physiological responses. In addition to environmental variables, response or performance variables must be carefully selected. Performance measurements can include vital rates, metabolic rates, or specific metabolite accumulation, and its selection will depend on our research question, scale of the study, and type of organism. Multivariate approaches can be also considered to integrate trade-offs in response curves (Evans et al. 2015, Fefferman and Romero 2013).

4) Physiological model: parameter estimation and model fitting. If the MNM is fitted using biophysical ecology, parameter estimation is required depending on our model complexity level (life-stages, energy and water balance, locomotion, etc. See point 3). For species response curves, both linear and non-linear or asymmetric physiological responses should be considered to properly capture the trade-offs organisms face under changing climates (Fenollosa and Munne-Bosch 2019b; Buckley et al. 2022). Selecting the appropriate equations for baseline 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. Some of the observed studies used convex functions (Fadda et al. 2024), a plateau model (Feng et al. 2020). In insects, the theorical temperature-dependent developmental rate curve is generally assumed to follow a unimodal shape, with a linearity zone before the optimal temperature (Rebaudo and Rabhi 2018). However, multiple models have been used to fit those curves, such as Logan-10, Lactin-2, Briere-2, Taylor, Beta models (Rebaudo and Rabhi 2018) showing slightly different projections at extreme temperatures. We must consider as well if we are interested in understanding species response to a wide environmental range, discrete conditions or if the physiological model will be used to extract only optimal, mean or limit points. Using at least five experimental conditions is common to fit a thermal curve (e.g. Lin et al. 2019; Pertierra et al. 2020; Fadda et al. 2024), but the experimental design will depend on the modelling aim. Temporal regimes must be considered, for example deciding if the physiological model is fitted with constant or cycling temperatures. 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, the next step is translating the physiological model into geographic space. This usually requires estimating environmental conditions experienced by the organism at relevant temporal and spatial scales (see point 3 above). This may involve using microclimate models to translate gridded climate data into predictions of historic, current or future microclimates, ideally considering behaviour and habitat use of the target organism (Kearney et al. 2020; MacLean et al. 2021). Our review revealed substantial diversity in the temporal and spatial resolution of environmental drivers, ranging from monthly air temperatures (e.g. Tablado and Revilla 2012) to hourly soil or air temperatures (e.g. Hartley et al. 2010; Chapman et al. 2014). The usage of ERA5 climatic data is recommended to build microclimatic models (Klinges et al. 2022). To evaluate climate change impact on invasive species distribution, a forecast of the chosen variable under different climate change scenarios must be acquired. The temporal resolution of environmental data is as important as its spatial resolution (Guisan et al. 2019). An MNM based on energy budget might still work at global scale, but an MNM based on physiology and fine-scale processes might not make much sense if applied to large scale based on very coarse environmental maps. We recommend reporting the variable used for the geographic projection as well as the rationale of the chosen temporal and spatial resolution when building MNMs. Once the potential distribution is obtained, we might be interested into comparing projected distribution areas (Vaughan and Ormerod 2005; Levine et al. 2009; Wilson 2011; Huang et al. 2018) and use it for a closer examination of specific regions, such as invasion hotspots, protected areas or range edges, can yield critical information on species spread, habitat suitability, and the effectiveness of management interventions. Finally, contrasting MNM with correlative SDM following standard procedures might be strongly informative to detect non-environmentally driven occurrences and further understand the invasion process (e.g. Higgins et al. 2020; Dormann et al. 2012).

6) Limitations acknowledgement. A final recommended step is to revise the whole modelling process and acknowledge potential limitations of the mechanistic model. A few examples that we might miss out when building MNMs (depending on how they are built) are dispersion, habitat availability, other species relevant interactions, further intraspecific variability, hysteresis responses, interaction between multiple environmental variables, impact of spatial and temporal resolution of the environmental variables and modelled processes, life stages considered, extreme events and memory or priming responses (See full description in Suárez-Seoane et al. 2017; Briscoe et al. 2019; Briscoe et al. 2023; Riddell et al. 2023). Sensitivity analysis can be used for unknown parameters and/or include trait variability into the model (Mitchell et al. 2016; Strubbe et al. 2023).

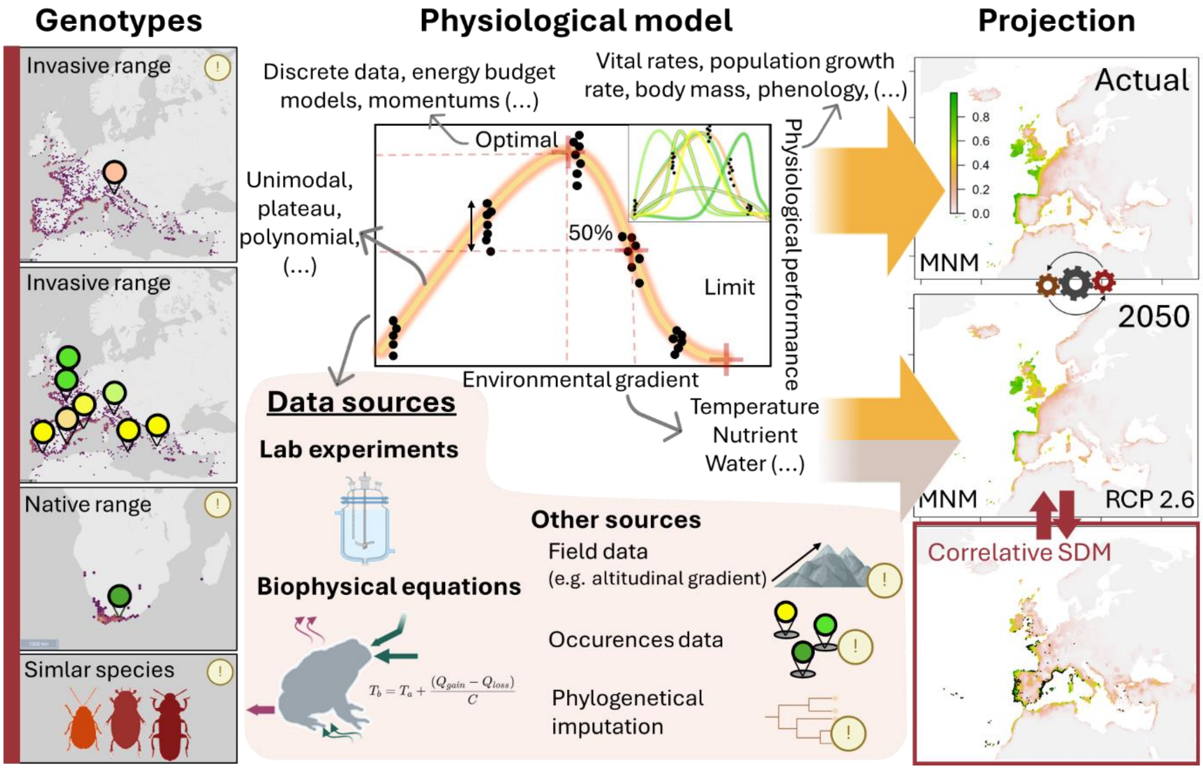


Figure 4. Elements to consider when building Mechanistic Niche models for invasive species, from genotype selection, the construction of the physiological model and geographic projection. Exclamation signs symbolise that by taking those approaches the model might not be suited for invasive species projections.

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

Beyond being limited to selected environmental drivers and available data, the limitation of MNMs is that, while they offer detailed, process-driven insights into species' physiological responses to environmental conditions, they may miss important fine-scale temporal and spatial information. This can include factors like microhabitat features, local competition, and biotic interactions that are often implicitly captured by correlative SDMs (Davis et al. 2024). MNMs excel at providing broad-scale predictions by linking species distributions to underlying mechanisms such as thermal tolerance, metabolic rates, or water balance (Kearney and Porter 2009). At the same time, if parametrized with fine-scale variables, MNMs are very useful at the range edge, where climate is limiting (Briscoe et al. 2016). However, it must be noted that sometimes species might occur beyond their physiological limits thanks to adaptative or facilitative mechanisms (Chevalier et al. 2024). Essential spatio-temporal invasion complexities such as human activity influences, like trade, transportation, urbanisation, and land-use changes, introduce additional layers of complexity that are not easily modelled through physiological limitations frameworks. In this section we will revisit whether MNM can overcome all the limitations of correlative SDMs for invasive species.

Overcoming correlative SDM limitations by MNMs is not an easy endeavour, especially for modelling large number of species (which SDMs can do, e.g. Adde et al. 2024, but see the mechanistic model built for 20 birds in Europe: Strubbe et al. 2023), an effort that will largely depend on how our MNM is constructed (**Figure 4**). Careful parameterisation is essential to ensure that MNMs address specific challenges associated with correlative SDMs in invasive species modelling. MNMs can overcome almost all correlative SDM limitations when our aim is to understand its potential distribution under novel climates (as well as the derived applications described in **Figure 3**). For applications such as estimating invasion speed or reconstructing the history of an invasion, MNMs alone are not the most suitable approach (Wilson et al. 2007), although estimated dispersal capacity from an MNM (e.g. Kearney et al. 2008) could be incorporated into spatially explicit models such as IBMs.

MNMs might fail when (1) predicting species distribution limits where species is not being limited by the environment, (2) a single environmental factor is used, and the species response strongly depends on the interaction with another (e.g. temperature and moisture), (3) model is not complex enough to capture real conditions the species is submitted to. This last point includes not selecting the proper temporal and spatial resolution and range of the modelled processes and environmental matching data, but also not capturing intraspecific or interpopulation variability.

Conversely, MNM will be better than correlative SDMs to predict future distribution when: (1) the species is on early stages of invasion and invasive region has a lot of novel environments not captured in native range, (2) it is known that biotic interactions are likely to be very different at the invaded range, (3) the species shows strong genetic diversity on the invaded range leading to identification complexities, (4) the species is used for commercial interests (i.e. planted trees) and are naturalized and not invasive in certain areas outside the native range, (5) time-lags are driving the invader expansion at the invaded range, (6) there are strong range-edge processes taking place. In case 3 and 6, the MNM must be fitted with representative genotypes across the invaded range and/or at range-edge.

Although the usage of hybrid models such as CLIMEX fitted using occurrence data might bypass data needs, the capacity of those models to respond certain research questions will be strongly limited depending on specifically how this model is populated. Models including data from invasive species occurrences, will not allow us to build predictions under novel conditions, especially on early invasion stages.

Other mechanistic approaches such as demographic distribution models, individual-based models or dynamic models are better fitted to simulate population responses after a specific perturbation, a management action or calculate invasion expansion rate (Briscoe et al. 2019). Domisch et al. (2018) further argue that spatially explicit modelling (i.e. considering spatially-explicit processes, such as in DDMs or occupancy dynamics models) is an underused tool in conservation planning, offering the potential to integrate species' distributions with habitat connectivity and management strategies Further steps would be the inclusion of genetic dynamics or evolutionary processes within SDMs and MNMs to capture species' adaptive potential, further improving the model's predictive power (García-Ramos and Rodríguez 2002; Kearney et al. 2009; Beninde et al. 2016; Bush et al. 2016).

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 decisions by explicitly considering the drivers of species distribution (Evans et al. 2015). MNMs are particularly suited for predicting potential distribution of invasive species as these organisms are often distributed across the landscape under non-equilibrium conditions that are difficult to simulate with 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 laboratory experimental data obtained by submitting considering trait multiple representative genotypes across the invaded range to a wide range of environmental predictors. However, such designs demand expensive and time-consuming experimental efforts, limiting their feasibility. While building fully mechanistic models may be impossible—given that the necessary experimental data will probably never be available, but also particularly given the context-dependent and spatio-temporal complexities of biological invasions (Laxton et al. 2022)— aim-oriented MNM for invasive species will definitely constitute better management tools than correlative SDMs to predict invasive species potential under climate change conditions at early invasion stages. Beyond the revised applications when MNMs would be a good choice, we also encourage the usage of MNMs to assess potentially invasive species risk under climate change.

Integrating phylogenetic signals can reveal evolutionary constraints on species' responses to novel environments (Wiens et al. 2009), 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).

SUPPLEMENTARY MATERIAL

Supplementary Material 1. Detailed procedure followed to conduct the systematic review.

Supplementary Material 2. Complete list of articles included in the systematic review, including all published articles using mechanistic niche models for invasive species up to the present date.

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Supplementary Material 1. Detailed procedure followed to conduct the systematic review.

To evaluate the existence of literature using mechanistic niche models to forecast invasive species distribution, we performed a systematic review. Due to the multiple terminology related to mechanistic niche models we compiled and deleted duplicates from multiple SCOPUS searches.

In 2019, Briscoe et al compiled all literature using process-explicit models until that date used for multiple purposes. Since here we focus exclusively on the potential of mechanistic niche models for invasive species, we used the literature list compiled by Briscoe et al. (2019) and filtered the studies evaluating invasive potential. Moreover, we used the search terms used to re-do the search and include the work published in the last 5 years. As Briscoe et al. did, we limit our search to studies that project the distribution of the species, with filtering studies that included in their title, keywords or abstract “species distribution model” or “occupancy dynamics” or the terms “geographic distribution”, “species distribution” or “species range". We included only research articles within the subject fields “Environmental science” and “Agricultural or biological science” or “Multiple” (We included ‘Multiple’ to capture articles in journals such as PLoS One, PNAS that publish research on a range of topics). The search was conducted on the 15th of September 2024. Despite the aim of the systematic review is to find all articles performing mechanistic niche models, we used the search terms from Briscoe et al. 2019 to acquire also demographic distribution models and individual-base models since as discussed in the review the limit might be a bit diffuse and we preferred to revise all articles in case a few might include estimates of the fundamental niche, which might categorize them as MNMs.

Type of process-explicit model	Scopus search terms	Number of items
Mechanistic niche models (or Ecophysiological models)	(TITLE-ABS-KEY (("species distribution model" OR "range dynamics" OR "occupancy dynamics" OR ("species distribution" AND predic*) OR ("species range" AND predic*) OR ("geographic distribution" AND predic*)) AND (ecophysiolog* OR eco-physiolog* OR mechanistic OR biophysical OR "physiolog* based" OR "physiolog* driven") AND (invasive* OR invader* OR *alien* OR non-native* OR neophy* OR neobiot* OR ias OR exotic* OR invasion OR pest*)) AND NOT SRCTITLE (human OR medic*)) AND (LIMIT-TO (SUBJAREA , "AGRI") OR LIMIT-TO (SUBJAREA , "ENVI") OR LIMIT-TO (SUBJAREA , "MULT") OR LIMIT-TO (SUBJAREA , "BIOC") OR LIMIT-TO (SUBJAREA , "EART")) AND (LIMIT-TO (DOCTYPE , "ar"))	107
Demographic distribution models	(TITLE-ABS-KEY (("species distribution model" OR "range dynamics" OR "occupancy dynamics" OR ("species distribution" AND predic*) OR ("species range" AND predic*) OR ("geographic distribution" AND predic*)) AND (demograph* OR "integral projection model" OR "matrix population model" OR "transition matrix" OR "population model" OR "population growth rate*" OR "vital rate*") AND (invasive* OR invader* OR *alien* OR non-native* OR neophy* OR neobiot* OR ias OR exotic* OR invasion OR pest*)) AND NOT SRCTITLE (human OR medic*)) AND (LIMIT-TO (SUBJAREA , "AGRI") OR LIMIT-TO (SUBJAREA , "ENVI") OR LIMIT-TO (SUBJAREA , "MULT") OR LIMIT-TO (SUBJAREA , "BIOC") OR LIMIT-TO (SUBJAREA , "EART")) AND (LIMIT-TO (DOCTYPE , "ar"))	139

Individual based models	(TITLE-ABS-KEY (("species distribution model" OR "range dynamics" OR "occupancy dynamics" OR ("species distribution" AND predic*) OR ("species range" AND predic*) OR ("geographic distribution" AND predic*)) AND ("individual based model*" OR "agent based model" OR individual-based OR agent-based OR ibm) AND (invasive* OR invader* OR *alien* OR non-native* OR neophy* OR neobiot* OR ias OR exotic* OR invasion OR pest*)) AND NOT SRCTITLE (human OR medic*)) AND (LIMIT-TO (SUBJAREA , "AGRI") OR LIMIT-TO (SUBJAREA , "ENVI") OR LIMIT-TO (SUBJAREA , "MULT") OR LIMIT-TO (SUBJAREA , "BIOC") OR LIMIT-TO (SUBJAREA , "EART")) AND (LIMIT-TO (DOCTYPE , "ar"))	25

Duplicated articles were identified and removed by DOI. Still 4 articles about medical treatments from the journals “Breast Cancer Research and Treatment” and “Cancer” were found and discarded. After removing duplicates and medical research articles, the total number of articles was: 235, from 1996 to 2024. However, about 50% of the articles did not actually include a mechanistic niche model in invasive species and contain only mechanistic diffusion for example or evaluated the correlation of invasive species abundance with a non-invasive target species when performing a correlative SDM. After individually checking all articles, only 97 were found to perform a MNM, demographic distribution, or individual-based model with one or more invasive species.

From those articles, we selected the ones that fit into the definition of MNMs: process-explicit models where measurements or calculations of physiological limitations of the environment on vital rates are used to define species’ range limits and used to project species potential distribution (Kearney and Porter, 2009; Evans et al. 2015). Demographic distribution models that were built solely from field data, and individual-based models that did not include environmentally explicit performance were discarded.

From those articles we recorded the following information: Species studied and their taxonomic group, whether the study was based on one or more species, aim of the study, name of the model used, type of the model, if climate change projections were included, which type of empirical data was used to parametrize the model, scale of the projection, captured processes and insights to advance in biological invasions forecasting.

The obtained list of articles can be found in **Supplementary Material 2**.