

ECOLOGY

Review

From niche theory to demographic realities: the demographic niche concept for understanding range-wide population dynamics

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The ecological niche concept is fundamental to understanding species distributions but often overlooks the demographic processes shaping said distributions. Conversely, demographic theory has traditionally neglected how vital rates vary and covary across environments, limiting our understanding of population dynamics across species' ranges. Over 50 years ago, Maguire proposed conceptualising the ecological niche as composed of multiple 'demographic niches' corresponding to separate vital rates such as survival, development, and reproduction. Although Maguire's perspective failed to gain prominence – constrained by the demography theory, data, and tools at the time – it provides a foundation we now expand upon. Here, we formalise the demographic niche concept (DNC), integrating Maguire's perspective with recent advances in niche theory and demography. We review the theoretical foundations of demographic niches, outline the tenets of the DNC, and define demographic niches (using phenology and ontogeny as guiding axes) and their boundaries (in terms of vital rate variation along environmental gradients). We then introduce a framework for visualising the arrangement of demographic niches in environmental and geographic space, clarifying how overlap or divergence shapes persistence across time and space, extinction debts under global change, or reveal intervention opportunities. We also propose the unimodal response hypothesis, predicting that vital rates peak at optimal conditions and decline toward margins, with deviations revealing additional ecological processes such as demographic compensation, density dependence, or niche truncation. Throughout this review, we discuss methods for modelling and integrating demographic niches and their relevance for addressing global challenges such as climate change. While data requirements remain non-trivial, this barrier is rapidly shrinking as demographic datasets grow, process-based models become more accessible, and remote sensing capabilities improve. By advancing the conceptual and methodological foundations of the



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DNC, this review establishes a basis for future empirical research and applications, offering new directions for ecological theory and conservation amidst a changing world.

Keywords: climate change, demographic distribution, environmental gradients, life history, niche modelling, vital rates

Between niche and demography

Why do species exist in certain areas and not in others (Sutherland et al. 2013)? In the face of biodiversity loss and ongoing global changes (Gibson et al. 2013, Maxwell et al. 2016, Pang et al. 2024), understanding the factors driving species distributions is more urgent than ever. The ecological niche concept holds part of the answer and is accordingly central to ecology, evolution, and conservation biology (Pulliam 2000, Chase and Leibold 2003, Holt 2009, Elith and Leathwick 2009, Peterson et al. 2011, Guisan et al. 2013). Hutchinson (1957) defined the ecological niche as an n -dimension hypervolume of environmental conditions that allow a species to persist, i.e. non-negative population growth rates. While qualitative (Murray 1866, Schimper 1902, Grinnell 1904) and envelope-style (Cook 1929, 1931) species distribution models (SDMs) existed earlier, Hutchinson's framing was foundational to modern interpretations and modelling of niche and distribution (Green 1971, Vandermeer 1972, Austin 1985, Pulliam 2000, Chase and Leibold 2003, Soberón and Peterson 2005, Pearman et al. 2008, Colwell and Rangel 2009, Elith and Leathwick 2009, Holt 2009, Soberón and Nakamura 2009). Today, SDMs are widely used to understand species–environment relationships, conduct threat assessments, and inform conservation decisions (Thuiller et al. 2005, Guisan et al. 2013, Peterson et al. 2018), typically relying on occurrence data to estimate the realised niche – where biotic interactions, abiotic conditions, and accessibility jointly permit persistence (Soberón and Peterson 2005, Peterson et al. 2011, Guisan et al. 2017).

Hutchinson's classical framework, however, does not mechanistically represent how niches are shaped by demographic processes – the vital rates of survival, development, and reproduction – which drive population dynamics. How vital rates vary across environments is critical to understanding range-wide population dynamics (Crozier and Dwyer 2006, Bykova et al. 2012, Merow et al. 2014a, Ehrlén et al. 2016, Csergő et al. 2017). Neglecting key vital rates can yield predictions that deviate from reality. For example, Merow et al. (2017) found nearly opposite climate responses when comparing occurrence-based versus demographic models, a discrepancy echoed by other studies (Carbeck et al. 2022, Dial et al. 2022, Perez-Navarro et al. 2022). Such discrepancies arise because occurrences do not necessarily reflect demographic performance, and because different vital rates can respond oppositely to the same environmental change – patterns that can also remain hidden in models focusing only on overall population growth (Fréville and Silvertown 2005, Caswell 2010, McDonald et al. 2016). These mismatches risks misinforming threat assessments and conservation planning

(Zurell et al. 2009, Svenning and Sandel 2013, Peterson et al. 2018, Pagel et al. 2020).

Long before these concerns emerged, Maguire (1973) proposed an explicitly demographic expansion of Hutchinson's niche: the niche as composed of multiple demographic response functions (demographic niches), corresponding to specific vital rates that collectively determine population growth (Fig. 1a). Despite Hutchinson (1978) lauding it '*the most important contribution to the concept of the niche since the death of Robert MacArthur*', Maguire's perspective remained largely overlooked, limited by the demographic theory, data, and modelling tools available at the time (but see Pulliam 2000, Holt 2009, Nenzén et al. 2012, Merow et al. 2014a, Ehrlén et al. 2016, Pironon et al. 2018). Meanwhile, demographic theory often focused on temporal variability in vital rates without explicitly linking them to spatial environmental gradients (Stearns and Koella 1986, Iles et al. 2019). Concepts like demographic buffering and lability – how populations may maintain (buffering) or vary (lability) vital rates under environmental stochasticity (Pfister 1998, Santos et al. 2021) – are rarely extended to large-scale environmental gradients (Hilde et al. 2020). We argue that this lack of ecological context has hindered further integration of demography into niche theory. The central gap and defining link between niche and demography is thus environment-dependent vital rate variation. Calls to bridge this divide have gone largely unanswered (Hutchinson 1978, Caughley 1994, Ehrlén et al. 2016). Still, resolving this gap is critical for understanding range-wide population dynamics and making robust forecasts under global change (Merow et al. 2014a, Ehrlén and Morris 2015, Pagel et al. 2020).

To address this gap, we reframe and formalise the demographic niche concept (DNC), building on Maguire's original perspective while integrating recent advances in niche theory and demography. We first clarify the theoretical foundations of the DNC and establish its core tenets, before exploring how demographic niches and their boundaries may be defined. We then introduce a framework for visualising demographic niches and their arrangement in environmental and geographic space, including their shifts under global changes. We also propose a starting hypothesis on how vital rates vary across environments – the current frontier of the DNC. Finally, we address key data and methodological challenges in applying the DNC, and explore other avenues for advancing the DNC. By coalescing and developing scattered ideas into a cohesive framework, we provide a clear conceptual foundation for linking demography with spatial ecology, laying the path for a more process-based understanding of range-wide population dynamics in a changing world.

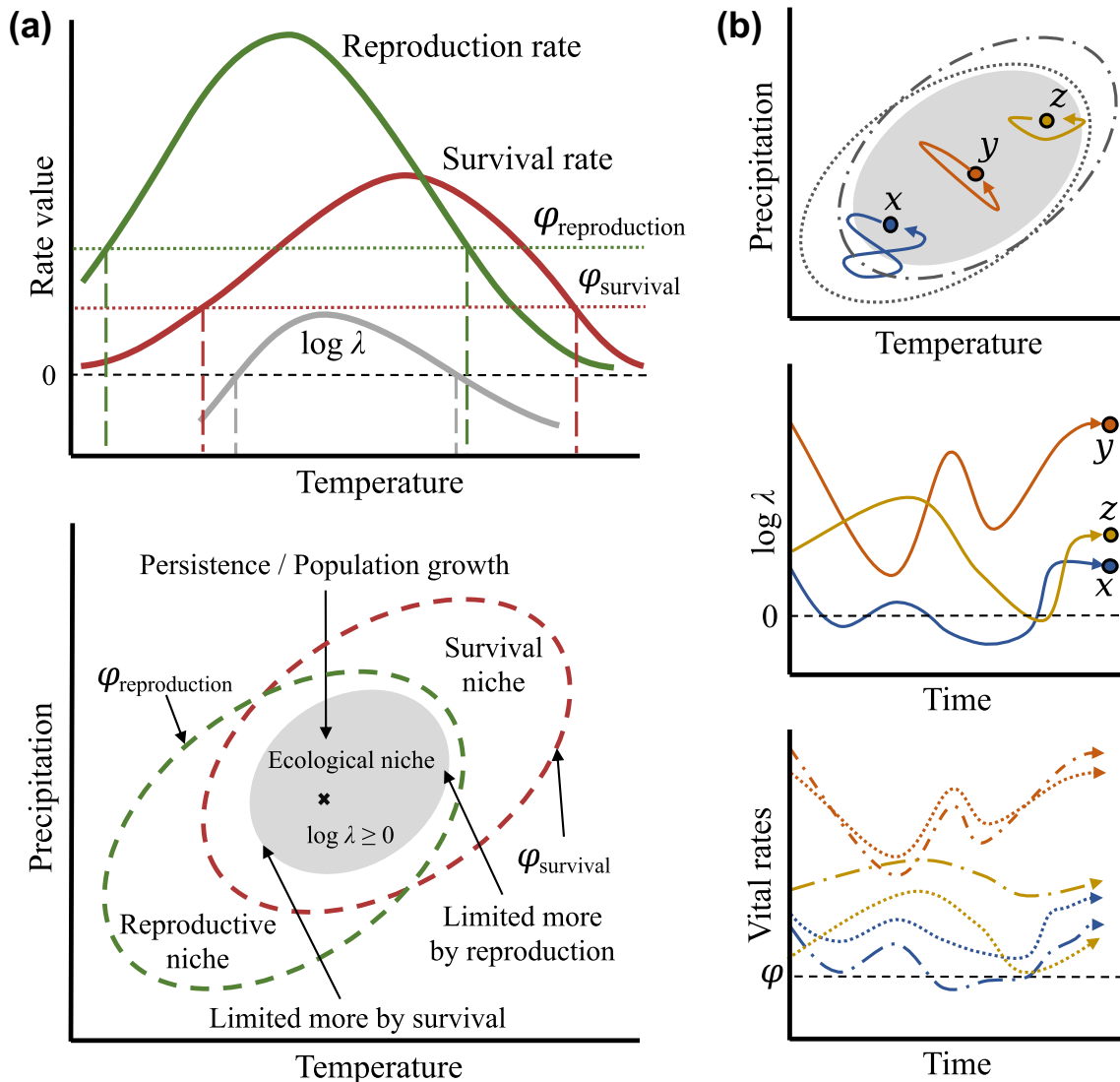


Figure 1. The ecological niche viewed through a demographic perspective. (a) The ecological niche (grey) in one (top panel) and two (bottom panel) dimensional environmental spaces, composed of two example demographic niches: a survival niche (red) and a reproduction niche (green). Vital rate responses for survival (red) and reproduction (green), and the resulting population growth rate $\log \lambda$ (grey), are shown along a temperature gradient (top panel), indicating how both vital rates decline from an optimal to reflect the shape and limits of each (demographic) niche; responses here were adapted from modelled simulations of a hypothetical annual plant with reproduction and juvenile survival rates responding unimodally to an environmental gradient (Data availability statement). The demographic niche boundary (dashed lines) indicates where the vital rate falls below the derived threshold, φ , the minimum vital rate value required to support population persistence while the other vital rate was held constant. For visual and conceptual clarity, a simple delineation of φ was used here; vital rate interdependencies among real populations are likely more complicated (see ‘*Defining demographic niche boundaries*’ below). Demographic niches therefore encompass the environments in which their vital rate could support persistence (vital rate $\geq \varphi$), where their overlap is necessary (but not always sufficient) for persistence ($\log \lambda \geq 0$), i.e. the ecological niche. The population growth rate, λ (Caswell 2001), is a dimensionless multiplier representing proportional change in population size per time step. While Hutchinson (1957) and Maguire (1973) described niches using the Malthusian parameter r (the difference between birth and death rates), our formulation relies on λ and its component vital rates (e.g. survival, reproduction), which is consistent with contemporary demographic modelling frameworks (Caswell 2001, Merow et al. 2014b). Under conditions of stationary equilibrium (Ebert 1999), $\log \lambda = r$, linking the two perspectives. (b) Abstraction of populations x , y , and z shown as points in environmental space, each experiencing temporally variable environmental conditions (shown as lines traversing said space) (top panel). This temporal variation results in fluctuating population growth rates ($\log \lambda$) over time (middle panel). Underlying these changes in population growth rates are vital rate responses to those environmental changes over time (bottom panel), where φ denotes the minimum vital rate value required to support population persistence, i.e. the demographic niche boundary. Note, vital rates in the bottom panel for real species are unlikely to share the same scale, and boundaries φ are unlikely to be similar between vital rates; vital rate variation and boundaries here were simplified for visual and conceptual clarity. Panels in (b) were adapted from Maguire (1973, pp. 220–221), specifically Fig. 6–7, with modifications for clarity and generalisation. Vital rates are shown primarily as abstract examples to provide a visual structure to the conceptualisation of demographic niches.

Inception of demographic niches

Constituent parts of the demographic niche concept

The niche dimension

Niche theory traditionally conceptualises niches as static hypervolumes limited by ‘external’ factors (Rangel et al. 2007). Soberón and Peterson’s (2005) BAM framework identified (B)iotic interactions, (A)biotic conditions, and (M)ovement or accessibility as the key constraints on species distributions – A defines the fundamental niche and BAM together defines the realised niche (Fig. 2a). Consequently, SDM advancements focused on improving or incorporating various environmental variables, such as soil conditions (Hageer et al. 2017, Corlett and Tomlinson 2020), temporally dynamic climate variables (Lalechère et al. 2025, Pang et al. 2025), anthropogenic factors (Requena-Mullor et al. 2019), and light regimes (Nieto-Lugilde et al. 2015, Pang et al. 2025). Following calls for considering biotic interactions (Araújo and Luoto 2007, Wisz et al. 2013, Anderson 2017), joint SDMs were developed to integrate co-occurrence patterns (Pollock et al. 2014, Warton et al. 2015b, Ovaskainen et al. 2016), albeit many cautioning against interpreting modelled relationships as true interactions (Godsoe et al. 2017, Dormann et al. 2018, Peterson et al. 2020, Poggiato et al. 2021; but see Holt 2020a). Others emphasised dispersal and accessible area constraints (Svenning and Skov 2004, Barve et al. 2011, Owens et al. 2013, Machado-Stredel et al. 2021), and accounting for dispersal capabilities when projecting range shifts (Bateman et al. 2013, Zurell 2017, Zanatta et al. 2020, Pang et al. 2024). Still, standard SDMs

fail to isolate the demographic processes driving range-wide population dynamics, obscuring mechanisms and sometimes misleading conservation planning (Dormann et al. 2012, Evans et al. 2016, Briscoe et al. 2019, Higgins et al. 2020, Pagel et al. 2020, Carbeck et al. 2022, Perez-Navarro et al. 2022, Tourinho and Vale 2023, Peng et al. 2024).

The demographic dimension

In contrast to niche theory’s ‘external’ focus, demography emphasises ‘internal’ processes, particularly how population growth is driven by multiple vital rates. Life cycle graphs depict life stages and transitions between stages, including transition probabilities and reproductive rates – the vital rates (Fig. 2b) (Caswell 2001). Vital rates are influenced by life-history strategy (i.e. the resource and energy investments in various life-history traits such as mode of reproduction and lifespan, e.g. perennial semelparity) (Stearns 1992, Salguero-Gómez et al. 2016b, Healy et al. 2019) and functional traits (i.e. morphological, physiological, or phenological characteristics that affect fitness, sensu Violle et al. 2007, e.g. specific leaf area) (Adler et al. 2014, Salguero-Gómez et al. 2018, Pistón et al. 2019). These vital rates can be combined to estimate population growth rates via structured population models, such as Life Tables (Boyce 1977) (states are age-based), Matrix Projection Models (Caswell 2001) (MPMs; states are age, development, or discretised ranges of size), or Integral Projection Models (Easterling et al. 2000, Ellner and Rees 2006) (IPMs; state is continuous, e.g. size). Vital rate contribution is calculated as the sensitivity (or elasticity when standardised) of the population growth rate to a small change – perturbation – in each vital rate (de Kroon et al. 1986,

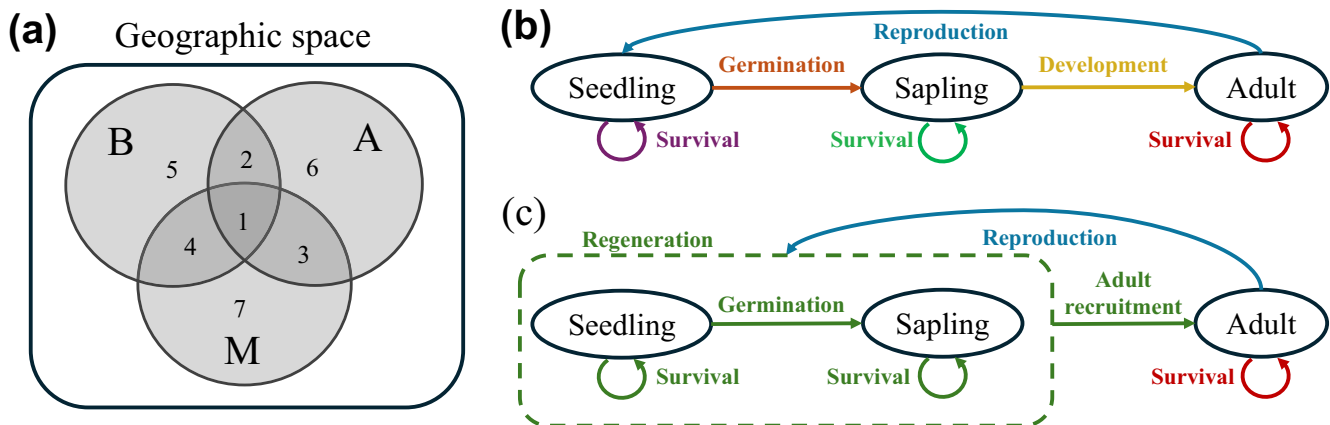


Figure 2. (a) The BAM concept, adapted from Soberón and Peterson (2005), describes the three factors constraining species distributions in geographic space: (B)iotic interactions, (A)biotic variables, and (M)ovement or accessibility. Venn overlaps indicate where these factors operate: (1) the realised niche; (2) suitable but inaccessible; (3) unsuitable because of biotic interactions; (4) unsuitable because of abiotic conditions; (5) with suitable biotic interactions only; (6) with suitable abiotic conditions only; and (7) accessible but unsuitable. (b) An example life cycle graph of a plant, depicting the stages of an organism’s life cycle and transitions between stages. Life cycle stages from seedling to sapling to adult are shown, with transitions highlighting the key vital rates. Beginning first with seedling survival, germination, sapling survival, development to reproductive maturity, adult survival, and then finally reproduction to produce seedlings; with each vital rate being coloured differently. (c) The same life cycle graph but with several vital rates related to regeneration – seedling survival, germination, and sapling survival – being consolidated under one regeneration niche and summarised simply as adult recruitment. Colours here indicate vital rate contribution to the regeneration (green), adult survival (red), and reproduction (blue) niche; vital rate colours here apply to Fig. 4.

Tuljapurkar et al. 2003, Caswell 2005). Demography has long considered spatial structures – such as in metapopulation models (Levins 1969, Hanski 1998), source-sink dynamics (Pulliam 1988, Pulliam and Danielson 1991, Amarasekare and Nisbet 2001), and the central-peripheral hypothesis (Brown 1984, Schurr et al. 2012, Pironon et al. 2017) – but it has rarely examined how interacting vital rates vary explicitly across environmental gradients to define a species' niche in a macroecological sense. Traditional demographic perturbation approaches often assume static vital rate distributions, fixed means, variance, and covariance between rates (Tuljapurkar and Orzack 1980, Caswell 2001, Villellas et al. 2015), overlooking how environmental changes over space or time might alter these rates (Doak and Morris 2010, Ehrlén et al. 2016, Merow et al. 2017). This oversight is particularly important in the context of climate change, where vital rate distributions are unlikely to remain static as populations are exposed to ongoing environmental shifts.

The integration between niche and demography

The 'external' versus 'internal' distinction of niche and demography is not absolute. Advances in trait-based SDMs (Pollock et al. 2012, Warton et al. 2015a, Ovaskainen et al. 2017, Benito Garzón et al. 2019, Chardon et al. 2020), phenology integration (Reed et al. 2010, Bajocco et al. 2021, Ponti and Sannolo 2023, Peng et al. 2024, Zurell et al. 2024), and mechanistic or process-based SDMs (Crozier and Dwyer 2006, Morin and Thuiller 2009, Zurell et al. 2009, Evans et al. 2016, Briscoe et al. 2019, 2023, Pilowsky et al. 2022, Tourinho and Vale 2023, Fenollosa et al. 2025), demonstrate growing efforts to meld the two. Similarly, IPMs (and MPMs to a lesser degree; Salguero-Gómez and De Kroon 2010, Erguler et al. 2022) can incorporate environmental variables (Teller et al. 2016, Ehrlén et al. 2016, Merow et al. 2017, Dial et al. 2022). Dahlgren and Ehrlén (2009) was the first to include an environmental covariate in an IPM while Merow et al. (2014a) developed the first full range model. Additionally, early efforts to quantify vital rate elasticities across environments have laid the groundwork for understanding how environmental context influences vital rates (Åberg et al. 2009, Salguero-Gómez and De Kroon 2010, Von Euler et al. 2014, Araújo et al. 2014). However, it is precisely this somewhat arbitrary 'external' versus 'internal' distinction that highlights the need to amalgamate concepts of niche and demography: both disciplines are essentially trying to understand the same ecological response – persistence – but through different perspectives.

Origins of demographically informed niches

Maguire (1973) argued that a species' niche is defined by its biological responses to environmental changes. He proposed a dynamic niche, structured by vital rates such as individual growth, maturation, and reproduction that vary across environments to collectively define a species' niche (Fig. 1a). The key distinction from the Hutchinsonian niche lies in the inclusion of demographic processes. Conversely, space distinguishes Maguire's perspective from traditional

demography. Maguire highlighted how a population's position within environmental (niche) space shifts over time, driving temporal changes in vital rates (Fig. 1b). Crucially, Maguire (1973, pp. 219–224) also recognised how populations of the same species experience different demographic responses under different environmental contexts, leading to inter-population variation in vital rates. This heterogeneity among populations, in turn, feeds back to shape temporal dynamics within any given population. It is this collective variation across environmental context and through time that defines a species' interaction with its environment, and thus its ecological niche and geographic distribution (Hutchinson 1978, Colwell and Rangel 2009). This dynamic perspective does not merely consider vital rate distributions in tandem with the ecological niche but explores how vital rate variability itself shapes the niche, integrating both concepts. Maguire's innovation was to recognise that vital rates are intrinsic to the niche itself, not just additional constraints.

A related but more stage-focused idea emerged slightly later through Grubb's (1977) regeneration niche, which emphasised the environmental conditions supporting germination, seedling survival, and growth to reproductive maturity (Fig. 2c), and its distinction from the survival niche of adult plants. This distinction aimed to explain species coexistence and diversity, where spatiotemporal environmental variation provides different regenerative opportunities that reduce direct competition. Grubb's idea seeded multiple offshoots that emphasised different dimensions of regeneration. Bond and Midgley's (2001) persistence niche highlighted post-disturbance survival and resprouting potential over seed-based regeneration in fire- or herbivory-prone ecosystems. Similarly, the seedling-recruitment niche, a subset of the regeneration niche, focused on seedling establishment and is commonly applied in restoration and seed ecology (Young et al. 2005, Larson et al. 2023). These frameworks intuitively explain how different life cycle stages of a species and vital rates together define a species' niche and distribution.

This view of demographic niches as distinct components subtly contrasts Maguire's perspective of the various vital rates as constituent parts of a whole niche. Grubb's work and its derivatives aligned more with community ecology, explaining species richness through demographic niche differentiation. In contrast, Maguire's work is rooted in Hutchinson's niche as a hypervolume in environmental space, but where the niche is shaped by the variation of multiple vital rates (Ehrlén et al. 2016, Pironon et al. 2018).

While Maguire's conceptualisation was pioneering (Hutchinson 1978), it did not gain widespread application, remaining largely theoretical. In contrast, Grubb's (1977) regeneration niche independently highlighted the role of demographic processes in determining plant distributions, and has become an important dimension in plant ecology and regeneration dynamics (Howe and Smallwood 1982, Denslow 1987, Condit et al. 2006, Grime 2006, Díaz et al. 2016, Larson and Funk 2016). However, the regeneration niche focused on a single phase of a plant's life cycle,

capturing only a subset of all the vital rates necessary for a species to complete its life cycle.

Renewed interest in demographic niches

In recent years, renewed interest in integrating demographic processes into niche theory has led to important empirical advances. Merow et al. (2014a) was the first to map vital rate variation across environmental gradients in geographic space, with others soon following (Merow et al. 2017, Pagel et al. 2020, Carbeck et al. 2022, Dial et al. 2022). As demographic data and modelling techniques improve (Dahlgren and Ehrlén 2009, Metcalf et al. 2013, Merow et al. 2014a, Salguero-Gómez et al. 2015, 2016a, Teller et al. 2016, Holden et al. 2021, Levin et al. 2021, Owen 2023), so has the accessibility of environmentally informed demographic models (Schurr et al. 2012, Pethybridge et al. 2013, Merow et al. 2014a, Ehrlén et al. 2016). Pironon et al. (2018) furthered this renewal as the first to explicitly visualise the inner demographic structures of the niche. These works, along with others developing demographically-informed range models (Evans et al. 2016, Briscoe et al. 2019, Higgins et al. 2020, Heiland et al. 2022, Tourinho and Vale 2023, Ponti and Sannolo 2023, Peng et al. 2024, Fenollosa et al. 2025), highlight the need to understand how demographic processes vary and interact across space and time to shape the ecological niche.

Despite these advances, a formal, generalised Demographic Niche Concept remains absent. Such a framework would help integrate demography into niche theory (Holt 2009, Pironon et al. 2018), distribution modelling (Merow et al. 2014a, Ehrlén et al. 2016), and macroecological studies (Ehrlén and Morris 2015, Briscoe et al. 2019, Holt 2020b), enhancing predictions of species' responses to environmental change and offering a more mechanistic basis for understanding distribution dynamics. Our DNC unites and advances Maguire's integrative perspective with Grubb's life cycle stage-specific insights to create a more comprehensive framework for understanding species distributions and coexistences.

Formalising the demographic niche concept

The demographic niche concept (DNC) defines the ecological niche as composed of multiple, distinct demographic niches, each representing a single or set of vital rate(s) and their responses to environmental variation. Meaning, the DNC views the ecological niche as the emergent property of various demographic processes and their responses to environmental gradients. This framing highlights the dynamic, context-dependent nature of vital rates, emphasising how they shape range-wide population dynamics (Ehrlén et al. 2016, Pironon et al. 2018). The DNC not only explores how vital rates interact to form the ecological niche (Maguire's view) but also identifies distinct, ecologically relevant demographic niches (Grubb's perspective). While Hutchinson (1957) and Maguire (1973) grounded ecological niches in the Malthusian parameter r – the net difference between per

capita birth and death rates – we adopt the discrete-time analogue λ , the finite rate of increase. Whereas r is a continuous rate with units (e.g. births minus deaths per individual per time), λ is unitless and represents the proportional change in population size between time steps ($N_{t+1} = \lambda N_t$). This framing, widely used in modern demographic models (Caswell 2001), defines persistence simply as $\log \lambda \geq 0$. Terminology has also shifted, with death rate (d) now more commonly expressed as survival probability (where $1 - \text{survival} = \text{mortality}$), further aligning demographic metrics with stage-structured modelling frameworks.

Four tenets of the demographic niche concept

The DNC differs from traditional niche and demographic theory, providing a more comprehensive perspective on how vital rates (co)vary together to shape ecological niches.

Multiple vital rates

The DNC requires examining all vital rates in a species' life cycle – minimally, stage-specific survival, reproduction, and transition probabilities (e.g. growth). In more complex life cycles, this might include seed banking (Paniw et al. 2018), migration (Barthold et al. 2016), or clonal reproduction (Salguero-Gómez 2018). Indeed, analysing a single vital rate, or fitness component, is insufficient to determine persistence or (local) extinction (Caswell 2001, Morris and Doak 2002). However, if one vital rate consistently dominates population dynamics across environments – e.g. highest elasticity (de Kroon et al. 1986, 2000) or informed by life history theory (Franco and Silvertown 2004) – focusing on it is justifiable for certain purposes (e.g. adult survival in turtles; Heppell 1998).

Environment-dependent variation

The DNC focuses on how vital rates vary across space and time in response to environmental changes. Environmental drivers often affect vital rates unequally – a given gradient (e.g. temperature) may alter survival without affecting reproduction, or vice versa (Rees and Ellner 2009, Merow et al. 2014a, Kunstler et al. 2021). Such rate-specific sensitivity underlie variation between populations in different environments and within populations experiencing environmental change (Ehrlén et al. 2016, Teller et al. 2016, Perez-Navarro et al. 2022). The DNC distinguishes these structured responses from those driven only by environmental stochasticity (unpredictable changes; Morris and Doak 2004, Tuljapurkar et al. 2009) or regular environmental fluctuations (year-to-year averages and standard deviations; Pfister 1998, Rees and Ellner 2009).

Interdependency between rates

Vital rates often covary across environmental gradients to shape demographic outcomes in complex ways (Doak and Morris 2010, Iles et al. 2019, Vilellas et al. 2021). These relationships can involve trade-offs (negative correlations, e.g. reproduction versus survival) or positive covariation, producing non-additive effects (van Noordwijk and de Jong

1986, Pfister 1998, Morris and Doak 2004, Vilellas et al. 2015, Metcalf 2016). The DNC explicitly considers such interdependencies, which may emerge from physiological limits, evolutionary history, or shared environmental pressures (Stearns 1992, Jensen 1996, Capdevila et al. 2022), and can be explored using models that estimate multiple vital rates jointly (e.g. IPMs; Easterling et al. 2000, Ellner and Rees 2006, Merow et al. 2014a). Understanding how survival, reproduction, and other rates vary and interact offers mechanistic insight beyond summary metrics like λ or r alone (Hooper et al. 2008, Holt 2009).

Mechanistic understanding of niches and distributions

The DNC emphasises a process-based perspective, where environmental conditions drive species distributions through their effects on vital rates and population dynamics. This contrasts with correlative SDMs, which typically ignore the demographic mechanisms that underpin occurrence patterns (Zurell et al. 2009, Dormann et al. 2012, Schurr et al. 2012, Briscoe et al. 2019, 2023, Pagel et al. 2020, Lee-Yaw et al. 2022). Process-based models like IPMs (Ellner and Rees 2006, Merow et al. 2014a) and individual- or agent-based models (Wiegand et al. 1999, DeAngelis and Mooij 2005, Grimm et al. 2017) represent vital rate-environment relationships explicitly, providing process-oriented insights into persistence or decline across environments. Even correlative approaches can enhance ecological inference when some aspect of demography is integrated (Dormann et al. 2012, Pironon et al. 2018, Bajocco et al. 2021, Zurell et al. 2024).

Defining demographic niches

Necessarily bounded

A core ecological principle is that niches are bounded in environmental space: population growth rates cannot increase indefinitely and must become negative beyond certain limits (Hutchinson 1957). Since vital rates drive population dynamics, their variation must also adhere to this principle (Maguire 1973, Holt 2009). While we cannot always know the exact shape of a demographic niche (Maguire 1973, Austin 1985, Blonder et al. 2014, Swanson et al. 2015, Osorio-Olvera et al. 2019, Soberón and Peterson 2020), it is generally bounded – barring the hypothetical ‘Darwinian demon’ capable of maximising fitness in all environments. This boundedness anchors the DNC in both classical and contemporary ecological niche frameworks and concepts (Hutchinson 1957, Soberón and Peterson 2005, Austin 2007, Sax et al. 2013, Guisan et al. 2014, Holt 2020b), supporting its relevance for predicting range dynamics and distributional shifts under global change (Guisan et al. 2013, Ehrlén and Morris 2015, Briscoe et al. 2019, Carscadden et al. 2020).

Exceptions to being bounded

However, exceptions exist, and knowing when they occur informs when this assumption of boundedness must be carefully considered. Maguire (1973) described two cases, which we develop.

Indifference to an environmental limit

Some species are indifferent to the absence or maximum limit of certain environmental factors, creating an apparently unbounded (demographic) niche along that axis – though it remains constrained by the environmental variable’s natural limit(s). For instance, while toxins like mercury decrease survival, species are indifferent to its absence (Maguire 1973, p. 218). Even for temperature, where vital rates are ‘surely’ zero at its lower bound (absolute zero), tardigrades can survive, albeit in an anhydrobiotic state with other vital rates halted (i.e. $\log \lambda < 0$) (Persson et al. 2011). Typically, indifference occurs along toxin gradients and is especially relevant for tolerance-related rates like survival, or development in indeterminate-growth species.

Functional ceiling (or the infinite nuts conundrum)

Maguire (1973, p. 219) illustrated a key edge case of niche limits with squirrels along a nut resource gradient: as nuts increase, demographic performance (λ) rises, but eventually plateaus – further increases in nuts yield no demographic gains. Though the gradient could extend indefinitely, the population’s response does not, creating the appearance of an unbounded (demographic) niche. Unlike indifference, unboundedness here stems from biological limits. For example, physiological ceilings, such as limited time (Poole et al. 2007) or processing capacity (Farquhar et al. 1980), akin to Holling’s type II functional response (Holling 1959). Alternatively, resource co-limitation under Liebig’s law of the minimum (Sprengel 1827, Liebig 1840), where another factor limits demographic performance despite increases in the focal resource (Harpole et al. 2011).

Identifying key environmental axes

These exceptions raise an important question: which environmental gradients most strongly shape vital rates and demographic niches, and are thereby most critical for understanding range-wide population dynamics and their shifts under environmental changes? A potential solution comes from Merow et al. (2014a); they explored how environmental perturbations influence vital rates and, in turn, population growth, thereby uncovering which environmental changes most impact population dynamics. Extending this ‘environment-based sensitivity analysis’ to an elasticity framework – measuring the proportional effect of changes in specific environmental variables on population growth – offers a systematic way to assess population vulnerability to specific environmental changes.

Phenology and ontogeny as key axes

How demographic niches are defined carries significant implications for modelling population dynamics and interpreting environmental constraints. Phenology and ontogeny are crucial for identifying which vital rates at which life cycle stage constitute distinct and ecologically meaningful demographic niches (Post 2019, Carscadden et al. 2020, Heiland et al. 2022, Ponti and Sannolo 2023, Zurell et al. 2024).

Phenology identifies transitions between life cycle stages that often depend on specific environmental cues or drivers unique to that transition (Post 2019). For example, many marine and migratory animals use separate, seasonally defined habitats for feeding and reproduction, resulting in phenologically distinct demographic niches (Smith and Stirling 1975, Zanden et al. 2013). In plants, masting – episodic, synchronised reproduction – also illustrates phenological niche differentiation (Ashton et al. 1988, Kelly and Sork 2002, Pearse et al. 2020), often with clear environmental triggers (Espelta et al. 2008, Koenig et al. 2016, Vacchiano et al. 2017, Numata et al. 2022). Disturbance events such as tree fall (Kobe 1999, Wright et al. 2003, Kitajima and Poorter 2008) or fire (Higgins et al. 2000, Måren and Vandvik 2009) can likewise create phenological windows that enable or trigger transitions such as rapid growth or recruitment.

Ontogeny, by contrast, describes how demographic processes vary across developmental stages, and how environmental drivers affect vital rates differently among stages (Werner and Gilliam 1984, Carscadden et al. 2020). Grubb's (1977) distinction between regeneration and adult survival niches reflected this idea, noting that the environmental factors driving seedling and sapling survival differed from their adult counterparts, often operating also at different temporal scales (Poorter 2007, Anderegg et al. 2013, Heiland et al. 2022). Ontogenetic niche shifts may arise also from stage-specific environmental requirements or shifts in diet and the environmental conditions required to support said diet (Olson 1996, Pennekamp et al. 2013).

Phenology therefore emphasises time-dependent environmental windows for key transitions, while ontogeny highlights stage-specific demographic constraints across environmental gradients. These axes are complementary: phenology defines *when* and *where* transitions occur; ontogeny informs *which* stages are most sensitive to *which* environmental factors.

What constitutes a demographic niche thus varies with species' life history and ecological context. In trees, the regeneration niche typically spans seed germination, seedling survival, and growth to reproductive maturity – sometimes approximated by recruitment above a size threshold (e.g. ≥ 10 cm DBH) (Grubb 1977, Kunstler et al. 2021). More detailed studies may define separate demographic niches for size-structured survival, growth, fecundity, fruit production, and seedling survival rates (Doak and Morris 2010, Merow et al. 2014b). Ideally, each vital rate with distinct environmental dependencies should form its own demographic niche. In practice, however, definitions often reflect trade-offs between biological relevance, data availability, and model complexity. Researchers must balance the granularity of niche definitions with life history knowledge and the ability to isolate independent demographic processes.

Defining demographic niche boundaries

Conceptually

Defining the boundaries of the demographic niche has conceptual and methodological implications. Conceptually, we meld

Maguire's described vital rate boundaries with Hutchinson's niche definition, linking both through demography. Maguire (1973) identified survival boundaries in environmental space as the point beyond which 'survival continues for less than any ecologically meaningful interval' (Fig. 3a–b). Building on Hutchinson's (1957) definition of the niche – the set of environments where population growth is non-negative – we construe 'an ecologically meaningful interval' as having the *capacity* to maintain population persistence ($\log \lambda \geq 0$) (Fig. 3c). Drawing from this, the demographic niche boundary may thus be defined as the limits of a given vital rate(s) for which it *could* support persistence (Fig. 1a).

Yet, a vital rate's capacity to maintain persistence depends on other rates. Development, reproduction, and recruitment, interact with survival along ontogeny via trade-offs that collectively determine population dynamics (Stearns 1992) (Fig. 3d–e). However, trade-offs may not always be evident in nature (Tavecchia et al. 2005, Herfindal et al. 2015, Paniw et al. 2019); positive covariations can emerge along environmental gradients, particularly when variation in resource acquisition obscures allocation trade-offs (van Noordwijk and de Jong 1986, Metcalf 2016) (Fig. 3d). Recognising both trade-offs and positive covariation is crucial, as boundaries must ultimately reflect realistic rate combinations (Fig. 3d). A straightforward approach to defining the boundary of a given demographic niche is to hold all other vital rates constant, typically at their highest value (as done in Fig. 1a). Doing so, however, ignores vital rate covariation and introduces overestimations. For example, assuming unrealistically high reproduction (Fig. 3e) can artificially widen the survival niche (Fig. 3f), making lower survival rates appear sufficient for supporting persistence when it only does so under those exaggerated reproduction rates. We thus add a qualifier, defining the demographic niche boundary as the limits of a given vital rate(s) for which it *could* support persistence, *given realistic combinations of other vital rates*. The demographic niche is then the set of environmental conditions that allow the given vital rate(s) to exist above that derived limit (Fig. 1a, 3f).

Maguire also acknowledged additional boundaries: a secondary, wider survival rate boundary for especially tolerant life-cycle stages (Fig. 3a–b) – e.g. seed banks awaiting fire (Måren and Vandvik 2009) or tardigrades in an anhydrobiotic state (Persson et al. 2011). These do not conflict with our primary definition as Maguire did not consider ontogeny, and survival should be treated stage-specifically (Boyce 1977, Ellner and Rees 2006). When defining boundaries, what constitutes the demographic niche itself bears equal importance.

Importantly, how the boundaries of the demographic niche are defined also shapes how their overlaps are interpreted. When boundaries are estimated by holding other vital rates constant, demographic niches are overestimated. Consequently, the overlap between demographic niches then does not strictly correspond to the ecological niche (where $\log \lambda \geq 0$), because the combined space captured would exceed the set of environments that truly permit persistence (as shown in Fig. 1a). Accounting for more realistic vital rate combinations can reduce this overestimation, but

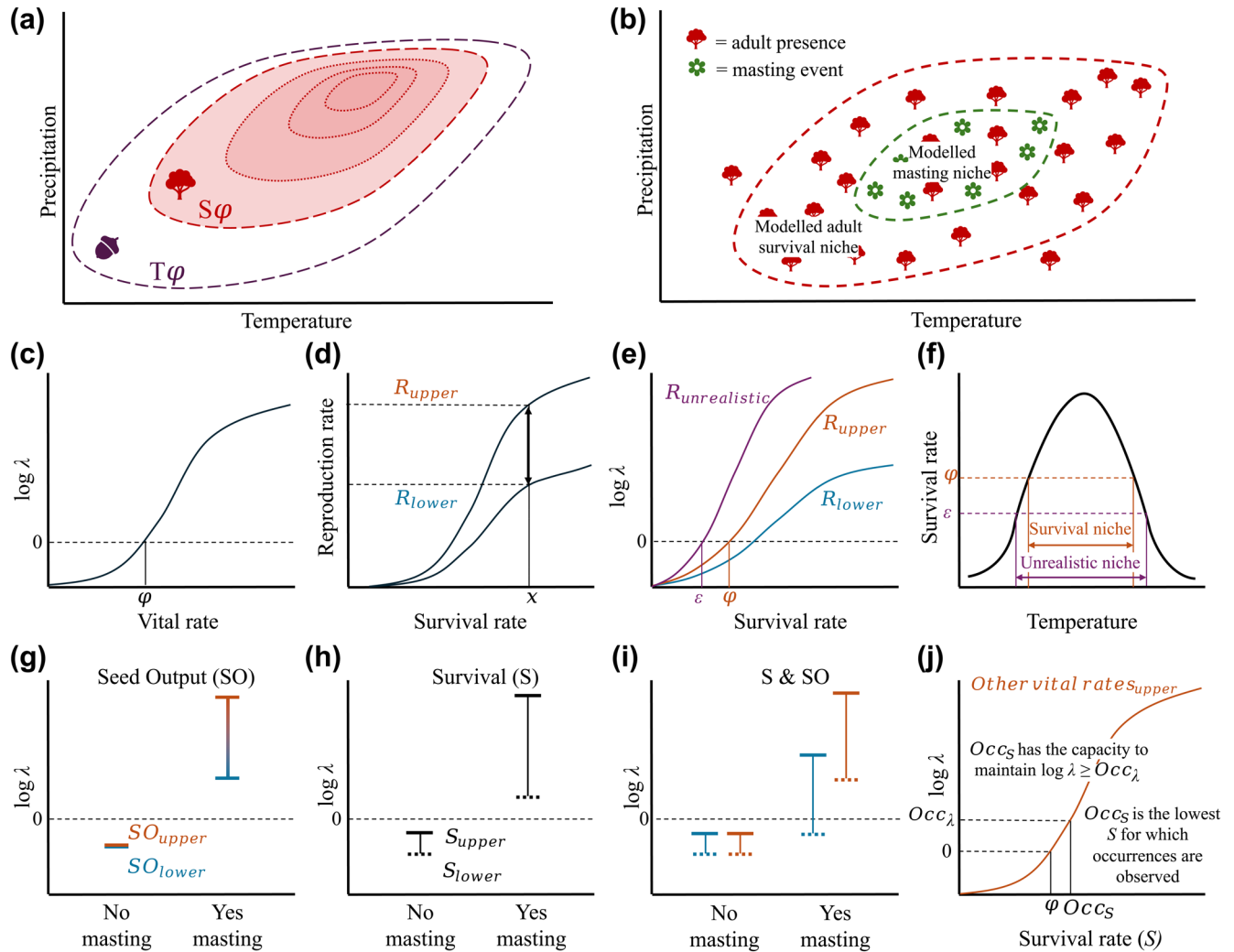


Figure 3. Defining demographic niche boundaries. (a) Illustration of survival rates (red isopleths; lines of the same value) in environmental space following Maguire (1973), where S_φ (red dashed line; red tree icon) marks the limit where ‘survival continues for less than any ecologically meaningful interval’, i.e. the survival niche boundary. A secondary tolerance boundary (T_φ ; purple dashed line; purple acorn icon) reflects an especially tolerant life cycle stage (e.g. seed stage). (b) Example mapping of adult survival (red dashed line) and masting (green dashed line) niches, with adult presences (red tree icon) and masting events (green flower icon) shown, in environmental space. (c) A vital rate mapped against population growth rate ($\log \lambda$), indicating the lowest value of a vital rate (φ) that maintains persistence ($\log \lambda \geq 0$), assuming no other vital rate. (d) Covariation between survival and reproduction, indicating realistic lower (R_{lower} ; blue line) and upper (R_{upper} ; red line) bounds of reproduction for a given survival rate (e.g. x). (e) Effects of survival on $\log \lambda$ given realistic lower (R_{lower} ; blue line) and upper (R_{upper} ; red line) reproduction rates compared to an unrealistic rate ($R_{unrealistic}$; purple line). The survival niche boundary – i.e. the lowest survival rate for which $\log \lambda \geq 0$ – is φ given realistic and ε given unrealistic reproduction rates. (f) Estimated temperature-dependent survival niche following realistic (φ ; orange) and unrealistic (ε ; purple) reproduction rates. (g) Population growth rate ($\log \lambda$) when masting occurs for a realistic lower (SO_{lower} ; blue) and upper (SO_{upper} ; orange) range of seed output (SO) values, such that where masting occurs, $\log \lambda \geq 0$ is true for all values of SO. (h) Population growth rates ($\log \lambda$) when masting occurs for a realistic lower (S_{lower} ; dotted) and upper (S_{upper} ; dashed) range of survival rate (S) values, such that where masting occurs, $\log \lambda \geq 0$ is true for all values of S. (i) Population growth rates ($\log \lambda$) when no masting occurs and when masting occurs for a realistic lower (blue) and upper (orange) range of SO values following (g), and for a realistic lower (dotted) and upper (dashed) range of S values following (h). For combinations of SO and S, $\log \lambda \geq 0$ is true for most combinations where masting occurs, though some low combinations of values result in $\log \lambda < 0$. (j) Occurrence derived survival niche, where only S is known. OCC_S is the lowest value of S for which occurrences are observed, obtained by mapping independent occurrence data against environmentally informed models of survival rates. Given the realistic upper bound of other vital rates (*Other vital rates_{upper}*; orange), OCC_S here is greater than φ , the true lowest value of S for which $\log \lambda < 0$, where the survival niche is underestimated. Here, populations where $S > OCC_S$ have the capacity to maintain $\log \lambda \geq OCC_\lambda$.

overlaps are still unlikely to precisely delineate the ecological niche, particularly as the dimensionality and complexity of environmental space increase. This difficulty with overlaps precisely delineating the niche reflects the fact that persistence emerges from nonlinear interactions among multiple vital rates (Maguire 1973, Ehrlén et al. 2016, Pironon et al. 2018), such that boundaries here represent marginal constraints rather than the full joint conditions required for $\log \lambda \geq 0$. Our overarching emphasis thus remains the full demographic response function (Fig. 4a) and their interactions

(Fig. 1a) – as originally envisaged by Maguire (1973) – since these responses capture both the shape and limits of demographic variation that underlie persistence. Nevertheless, we argue that examining the boundaries of the demographic niche remains informative: overlap among demographic niches is required for persistence, even if it is not a sufficient condition. As such, boundaries provide a useful and tractable framework for identifying which demographic components constrain persistence, analogous to Grubb’s (1977) regeneration niche.

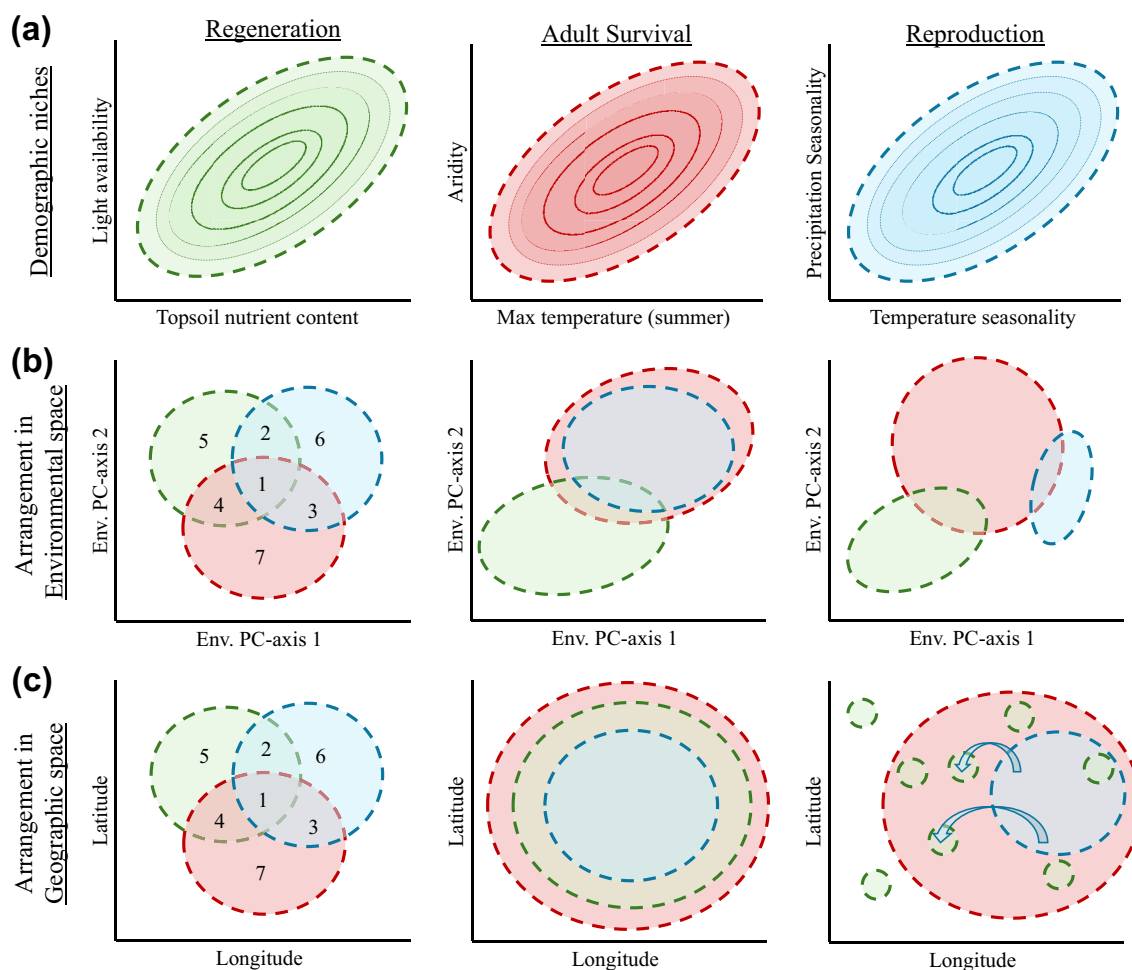


Figure 4. Visualisation of three demographic niches as defined by and coloured to match the life cycle graph in Fig. 2c. (a) The response surfaces of the Regeneration (left panel), Adult Survival (centre panel), and Reproduction (right panel) niche in separate, distinct environmental spaces (particularly the regeneration niche). Isopleths (lines of the same value) indicate vital rate variation within each demographic niche. (b) The arrangement of demographic niches in shared environmental space, as derived from a principal component analysis. Demographic niches in a hypothetical arrangement (left panel), with the regeneration niche diverging (centre panel), and with the regeneration and reproduction niche diverging and without any overlap (right panel). (c) The arrangement of demographic niches in geographic space, as demographic distributions, along some shared, determined spatial and temporal resolution of environmental conditions across said geographic space. Demographic distributions in a hypothetical arrangement (left panel), with a concentric arrangement (centre panel), with diverging demographic distributions (right panel). Panel right shows the sporadic occurrence of regeneration-suitable spots owing to local variability in environmental conditions (e.g. disturbance-driven changes in light availability), and reproduction for a given time step due to inter-annual variation in temperature and precipitation seasonality with arrows indicating the dispersal of seedlings into regeneration-suitable sites. (b–c) Venn overlaps indicate the suitability of each demographic niche/distribution: (1) where all life cycle stages are supported; (2) adult survival is limiting; (3) where remnant populations can reproduce but not regenerate; (4) where reproduction does not occur but populations may persist by relying on the dispersal/immigration of seeds/young; (5) where only regeneration may occur; (6) where only reproduction may occur; (7) where remnant populations survive but cannot reproduce or regenerate.

Methodologically

Estimating demographic niche boundaries means calculating the limits at which a focal vital rate could maintain persistence ($\log \lambda \geq 0$) under realistic combinations of other rates. Here, we describe estimation within an IPM framework (Easterling et al. 2000), but our approach applies to other population models as well, including life tables (Boyce 1977) and matrix population models (Caswell 2001).

First, calculate the deterministic λ across realistic combinations of vital rates – deriving λ for multiple parameter combinations from the IPM while preserving observed correlations among rates (e.g. survival, growth, and reproduction). This step is akin to generating a posterior predictive distribution from a Bayesian model (Ellison 2004), where all possible parameter combinations are explored to simulate a range of population dynamics. The boundary of the focal vital rate (e.g. survival) is then the limits of its marginal distribution for which persistence is supported. Crucially, boundaries are *context dependent* – e.g. an adult survival niche boundary of 0.2 does *not* imply persistence for any population with adult survival = 0.2; rather, persistence is possible at 0.2 *given* realistic combinations of other vital rates.

Direct observations of all rates are often unavailable. In such cases, inferred relationships among rates (e.g. via environmental covariates or population-level data) can be used, as demonstrated by Merow et al. (2014a) and Bernard et al. (2024) using an IPM. Although inferred relationships could allow for some unrealistic rate combinations, they still yield boundaries that are more mechanistic and biologically informed than those ignoring rate interdependencies altogether. For example, fixing non-focal vital rates at values that maximise $\log \lambda$ simplifies estimation but will almost certainly both include unrealistic and excluded realistic vital rate combinations. Moreover, resultant boundary estimates deviate from our formal definition because they no longer reflect the interdependencies among vital rates. Accounting for correlations remains crucial for more mechanistic and realistic assessments of demographic viability across landscapes.

Pragmatically

Our formal definition is grounded in demographic theory and data. However, applying this rigorous definition requires complete demographic information across vital rates and life stages – a requirement rarely met in practice. Certain vital rates, particularly those associated with early life stages (e.g. juvenile survival) or sporadic phenological events (e.g. tree masting), are difficult to observe. These challenges motivate pragmatic approximations using incomplete or simplified demographic data and models that still adhere to DNC's tenets.

When comprehensive demographic data are unavailable, practitioners may focus on key vital rates as proxies for persistence. For example, masting – an episodic, synchronised reproductive event common to many southeast Asian tropical trees species – can signal viability (Ashton et al. 1988, Numata et al. 2003, Pearse et al. 2020, 2021) (Fig. 3b). Assumptions about rate interdependencies can then be made:

1) seed output following masting is assumed to be sufficient to maintain population persistence (Fig. 3g); 2) in long-lived trees, adult survival is high enough that adult presence indicates a viable survival rate for that environment (Fig. 3h). Hence, masting presence or presence-absence can be modelled using SDM approaches to delineate the masting niche (Bajocco et al. 2021) (Fig. 3b), capturing conditions where masting occurs under assumingly realistic combinations of seed output and adult survival (Fig. 3b, i). Additionally, following assumption (2), independent occurrence data may be mapped against environmentally-informed projections of adult survival rates to estimate adult survival niche boundaries via SDM thresholding approaches (e.g. 95% of occurrences; Liu et al. 2016, Osorio-Olvera et al. 2019) (Fig. 3b, j).

Although λ across the full space of vital rate combinations remains unobtainable, focusing on one or several key rates – such as masting and adult survival – can still provide demographic insights across environments. Certainly, the set of rate combinations for which $\log \lambda \geq 0$ may not be explicitly calculated, but it can be *inferred* when populations fall within the observed masting and adult survival niche (Fig. 3b). Consequently, this vital rate thresholding approach allows for the approximation of demographic niche boundaries even in the absence of complete demographic data. This pragmatic approach, however, is not without caveats. Estimating the boundaries of one vital rate (e.g. masting) without direct knowledge of other rates (e.g. seed output) or the complete absence of other rates (e.g. recruitment) will lead to some overestimations (Fig. 3i, j). Assumptions about realistic rate combinations therefore require careful consideration of how interdependencies may influence population dynamics and should be clearly stated and justified.

Additionally, empirical demographic data are typically collected from persisting populations, meaning that observed vital rate variation is somewhat conditional on being within the ecological niche ($\log \lambda \geq 0$). Consequently, portions of demographic niche space associated with non-persistence are undersampled or entirely unobservable. Estimating demographic niche boundaries therefore necessarily involves extrapolating beyond observed combinations of vital rates, guided by theory, model structure, and inferred rate interdependencies (Stearns 1992, Jensen 1996, Merow et al. 2014a, Capdevila et al. 2022). This conditionality does not undermine demographic niche inference, but it does emphasise the need to interpret boundaries as inferred limits rather than directly observed thresholds. Experimental data, such as transplant or green-house experiments, are particularly valuable for exploring demographic niche spaces of non-persistence (Sax et al. 2013, Villellas et al. 2021).

Applying the demographic niche concept

Arrangement of demographic niches and distributions

A key novelty of the DNC is the opportunity to examine how demographic niches are arranged in environment and geographic space. Visualising the relative positioning, breadths,

and overlaps among demographic niches can elucidate how they interact, how those interactions vary across space and time, and how they change under global change (Maguire 1973, Pironon et al. 2018). Such arrangements provide an intuitive way to identify vital rate-specific drivers of population dynamics, particularly in geographic space, such as range-edge processes or source–sink dynamics (Ehrlén et al. 2016, Teller et al. 2016, Merow et al. 2017, Dial et al. 2022). While ecological niches are defined in environmental space, their geographic counterpart – i.e. Hutchinson’s duality, the reciprocal correspondence between environmental and geographic space (Hutchinson 1978, Colwell and Rangel 2009) – underpins the utility of SDMs (Soberón and Peterson 2005, Elith and Leathwick 2009, Guisan et al. 2013).

We present a framework for visualising the DNC in ecology, evolution, and conservation by borrowing concepts from niche and demographic theory (Maguire 1973, Caswell 2001, Soberón and Peterson 2005). The BAM framework helps identify how vital rates are constrained by (B)iotic interactions (e.g. pollinator for reproduction), (A)biotic conditions (e.g. soil conditions for saplings), or (M)ovement or accessibility (e.g. isolation of nesting sites) across geographic space (Fig. 2a). A life cycle graph, in turn, pinpoints relevant life-cycle stage(s) and vital rates – be it a single (e.g. adult survival) or set of rates (e.g. Grubb’s regeneration niche) (Fig. 2b–c) – that define demographic niches along environmental axes (Fig. 4a). Variation in these rates can be represented as isopleths – lines of equal value – within niche space (Fig. 4a) (Maguire 1973).

Visualising niches and distributions

Demographic niches can be represented in shared environmental space (Pironon et al. 2018, Pagel et al. 2020), for example using dimensional reduction (Fig. 4b). These visualisations isolate the breadth of environments required to complete different life cycle stages. Non-overlaps indicate environments where stages are unsupported, with differing implications depending on species’ mobility. Mobile or migratory species can traverse these gaps geographically (Smith and Stirling 1975, Zanden et al. 2013), emphasising (seasonal) migrations (Fig. 5a) (Zurell 2017, Post 2019, Carbeck et al. 2022). Comparatively, sessile species depend on overlapping or proximate environmental conditions to complete their life cycle (Fig. 4b), but some span gaps by sustaining one vital rate through time to enable another (Fig. 5a) (Ellner and Rees 2006, Lambers and Oliveira 2019, Post 2019, Carscadden et al. 2020). Fire-adapted seeds in the Mediterranean may persist in seed banks until post-fire germination (Pausas and Keeley 2014), while tropical saplings can remain in a stagnant growth stage until a canopy disturbance allows growth (Kobe 1999, Wright et al. 2003). In such cases, individuals effectively ‘move’ through environmental space via disturbance-driven changes.

Alternatively, or complementarily, demographic niches can be projected onto geographic space as demographic distributions (Merow et al. 2014a) (Fig. 4c), illustrating how demographic processes manifest across landscapes.

Non-overlapping demographic distributions identify which vital rate(s) drive local declines, offering insight into spatially explicit, vital rate-driven, source-sink dynamics (Merow et al. 2014a, 2017, Carbeck et al. 2022, Dial et al. 2022), which is useful for threat assessments and management planning (Sax et al. 2013). For instance, climate change may shift the reproduction niche distribution, leaving populations in survival-only areas (Fig. 5b), where long-lived species may persist as remnant populations, creating extinction debts often overlooked by SDMs (Dormann 2007, Dullinger et al. 2012, Svenning and Sandel 2013, Carlson et al. 2013; but see Rumpf et al. 2019, Lalechère et al. 2025, Pang et al. 2025). Concurrently, areas currently supporting only survival but projected to support reproduction could be flagged for interventions such as assisted migration (Iverson and McKenzie 2013).

When populations cross demographic niche boundaries in environment or geographic space (Fig. 4) and transition from persistence to decline, a key diagnostic question is which vital rate(s) drive this shift. In structured populations, this attribution problem aligns naturally with retrospective life table response experiments (LTREs), which decompose differences in population growth into contributions from individual life cycle stages and their underlying vital rates (Caswell 2010, Hernández et al. 2023). When coupled with environmentally informed demographic models (e.g. IPMs), LTREs can also partition those contributions among environmental drivers to reveal through which vital rates drivers act most strongly. LTRE-style analyses therefore provide a way to attribute boundary crossings and to link spatial or environmental transitions directly to demographic processes within the DNC.

Stitching of demographic niches

A key follow-up then is to focus on the more dynamic perspective: considering how populations connect disjunct demographic niches and distributions across space and time (Zurell et al. 2009, Zurell 2017, Post 2019, Pagel et al. 2020) (Fig. 5a–b). Temporal projections reveal how environmental fluctuations influence critical life cycle stages – for example, spatiotemporal variation in masting or gap-dependent recruitment (Brokaw 1985, Numata et al. 2003, Wright et al. 2003, Espelta et al. 2008, Bajocco et al. 2021, Foest et al. 2025). Tracking demographic distributions over fine (e.g. seasonal), inter-annual (e.g. El Niño–Southern Oscillation), or longer (e.g. climate change) timescales can also reveal transient dynamics that govern long-term persistence (Ezard et al. 2010, Svenning and Sandel 2013, Yackulic et al. 2015, Chapman et al. 2017, Bauman et al. 2022, Dial et al. 2022, Chisholm et al. 2024, Anujan et al. 2026). Temporal projections therefore help visualise how individuals or populations move across spaces to access various demographic niches – whether by physically migrating or via especially tolerant life stages – paralleling ideas on the phenological niche (sensu Post 2019).

Analogously, dispersal – including rare stochastic long-distance dispersal (Willner et al. 2023) – can drive large-scale range dynamics and critically shape both near-future

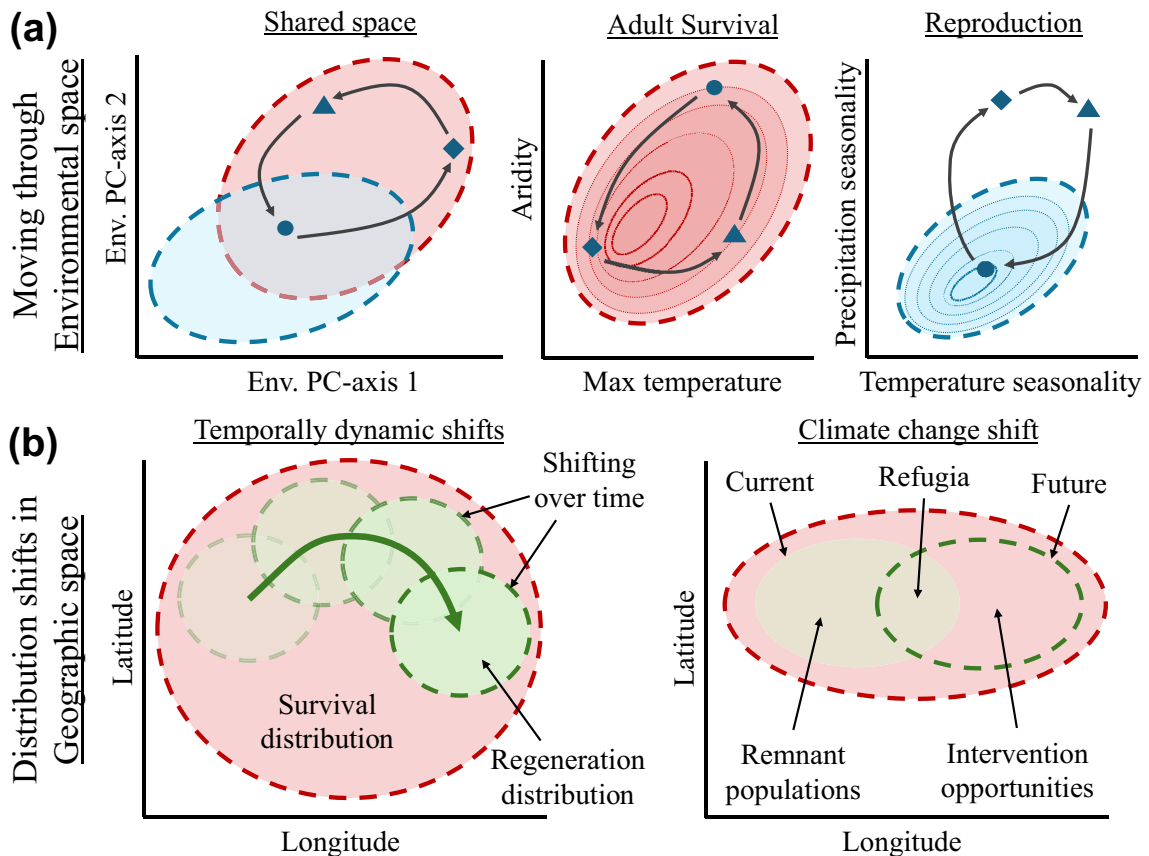


Figure 5. Visualisation of how populations experience environmental changes through their movement through, or the movement of, demographic niches. We focus on two example demographic niches for each space. We illustrate (a) individual or population movement through environmental space, and (b) demographic distribution shifts in geographic space. This distinction reflects that individuals more often navigate environmental conditions (e.g. via movement or phenological timing), whereas changes in spatial patterns due to environmental changes are best visualised geographically; however, either form of movement may be represented in both spaces. (a) The cyclical movement of an individual or population over time within the Adult Survival and Reproduction niche spaces at three time points (triangle, circle, and diamond). Movements may arise from physical displacement (e.g. green turtle migration to breeding sites) or local environmental changes (e.g. trees persisting until masting conditions arise). There is value both in visualising movement in shared space (left panel), offering a composite view of how an organism navigates environments to complete its life cycle, and within each demographic niche separately (centre and right panel), revealing more precise vital rate-environment relationships without space distortion. Note, the direction and environmental distance traversed between points varies between environmental spaces. (b) The geographic shifts in the regeneration distribution within the survival distribution. Temporally dynamic shifts (left panel), showing how regeneration opportunities move over time (e.g. opening and closing of canopy gaps within tropical forests). Climate-driven shifts (right panel), for beech trees as an example, showing how regeneration potential shifts geographically, creating areas of declining suitability (potential remnant populations) and areas of emerging suitability (potential intervention sites). We use ‘intervention opportunities’ here to highlight conservation implications but they represent areas where demographic shifts may enable persistence under future climate change.

projections (Svenning and Sandel 2013, Zurell 2017, Pagel et al. 2020) and longer-term modelling (Svenning and Skov 2004, Qiao et al. 2016). Under global change, the suitability of areas supporting particular vital rates shift geographically (Fig. 5b), while populations move across environmental space and the corresponding isopleths of vital rate variation (Fig. 5a). In both space and time, persistence depends on how organisms traverse or stitch together disjunct demographic niches. This echoes Holt’s (2009) ‘stitching the niche’ – the realised niche as stitched from a patchwork of suitable conditions at the metapopulation scale – but our framework focuses on individuals and populations. Both perspectives underscore the inherently dynamic assembly

of realised niches in equally dynamic environments, though they emphasise different scales and mechanisms.

Further applications

Explicitly mapping demographic niches offers more than descriptive insight – it provides a flexible, theory-driven scaffold for ecological forecasting and evolutionary inference. By separating vital rate-specific constraints across space and time, the framework helps disentangle the demographic mechanisms behind source–sink dynamics (Merow et al. 2017, Dial et al. 2022), extinction and colonisation lags (Svenning and Sandel 2013, Alexander et al. 2018), and range-edge limitations (Teller et al. 2016, Kunstler et al.

2021). Crucially, it shifts forecasting from relying solely on occurrence-environment correlations – or even population models that treat λ as the single response variable – toward process-explicit diagnosis, identifying which life stages or vital rates limit persistence under environmental change, and where stage-specific interventions (e.g. assisted regeneration or protection of reproductive sites) might be most effective. Forecasting must encompass all demographic niches contributing to λ , since persistence depends on their joint performance; focusing on one or two rates may suffice only for trait or life-history questions.

Relatedly, the arrangement of demographic niches invites deeper evolutionary questions on how life-history traits shape arrangements and species' vulnerability to climate change (Pagel et al. 2020, Villedas et al. 2021, Buckley and Puy 2022). For example, how demographic trade-offs drive niche divergence or specialisation (Doak and Morris 2010, Villedas et al. 2015, Carscadden et al. 2020), how natural selection acts on stage-specific responses across heterogeneous landscapes (Stearns and Koella 1986, Sexton et al. 2009, Coulson et al. 2011, Liu et al. 2020, Carley et al. 2025), or more fundamentally, why divergent demographic niches arise at all (Grubb 1977, Condit et al. 2006, Doak and Morris 2010). While the DNC is not in itself an evolutionary framework, it opens new pathways for testing evolutionary hypotheses about (demographic) niche structure and persistence in changing environments.

A fundamental hypothesis on vital rate variation

Unimodal response to environmental changes

Understanding how vital rates vary across environmental gradients is central to advancing the DNC. While previous work has largely focused on temporal variation within populations, the DNC emphasises how vital rates differ across populations in different environments, highlighting a critical gap in understanding and predicting population dynamics and species distributions (Merow et al. 2014b, Ehrlén et al. 2016, Buckley and Puy 2022, Carley et al. 2025).

We hypothesise that vital rates generally follow a unimodal response (concave) to environmental gradients (Fig. 6a). A unimodal curve, as a biological response, is often considered realistic, and underpins many recommendations for SDM parameterisation (Austin 2007, Merow et al. 2013, Drake 2015, Morales et al. 2017, Guevara et al. 2018, Citores et al. 2020). This unimodal expectation also parallels the abundant-centre hypothesis – the decline in abundance or demographic performance with increasing distance from an optimal centre, i.e. unimodal (Brown 1984). Despite challenges to the abundant-centre hypothesis in geographic space (Sagarin and Gaines 2002, Sexton et al. 2009, Pironon et al. 2015, 2017, Ten Caten and Dallas 2025), there is increasing support for it in environmental space (Yañez-Arenas et al. 2012, Martínez-Meyer et al. 2013, Weber et al. 2017, Osorio-Olvera et al. 2020, Broennimann et al. 2021, Perez-Navarro et al. 2022; but see Pironon et al. 2015, Dallas et al. 2017, Santini et al. 2019, Chevalier et al. 2021).

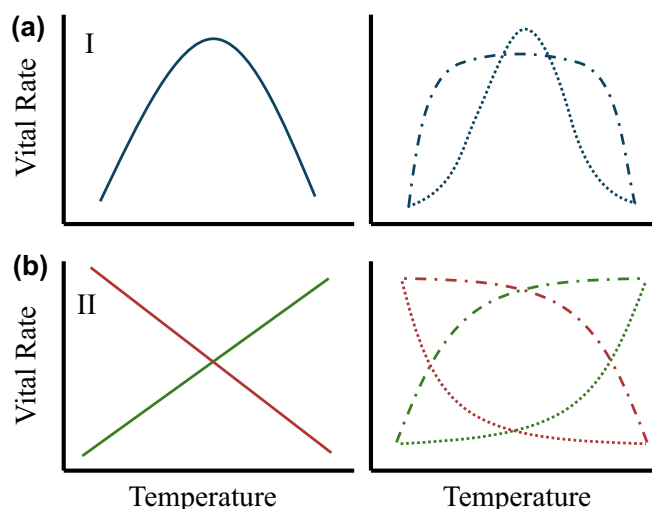


Figure 6. A visual representation of the hypothesised way in which vital rates may vary along an environmental gradient. (a) Vital rates follow a unimodal response, forming a concave response curve. A single vital rate determines the lower and upper boundaries of a hypothetical demographic niche along an environmental gradient. The unimodal response may peak at one singular most suitable environment and decline gradually from this peak (left) or follow other response types (right). (b) Vital rates follow a monotonic function but covary against another vital rate due to demographic compensation, forming a negatively correlated response to an environmental gradient. The two covarying vital rates combine to determine the lower and upper limit of a hypothetical demographic niche along an environmental gradient, where they together comprise the unimodal response, i.e. contribution to population growth rate. The monotonic function may be linear (left) or non-linear following other response types (right).

At apparent odds with this unimodal expectation is that vital rates increase with increasing distance from a supposed optimal centre (Chapin III and Shaver 1996, Arft et al. 1999) or vary monotonically (e.g. linearly) along environmental gradients (Fig. 6b). Such observations may be considered unrealistic, as a given vital rate cannot increase indefinitely or remain high nearing the margins of the ecological niche, all else being equal. Hence, studies have suggested demographic compensation to explain this opposing phenomenon, whereby the change in one vital rate are compensated by the opposite change in another vital rate (Doak and Morris 2010, Villedas et al. 2015, Sheth and Angert 2018). We thus relax our hypothesis such that the unimodal response may comprise a set of these negatively covarying vital rates. For example, seedling production and recruitment success may covary negatively, together forming a reproduction niche that still produces an overall unimodal response despite their individual monotonically changing rate.

Deviation from a unimodal response

The unimodal hypothesis provides a useful baseline for theory and modelling, but real-world observations often deviate (Pironon et al. 2015, Simon and Amarasekare 2024). While a theoretical optima may exist, real populations may instead

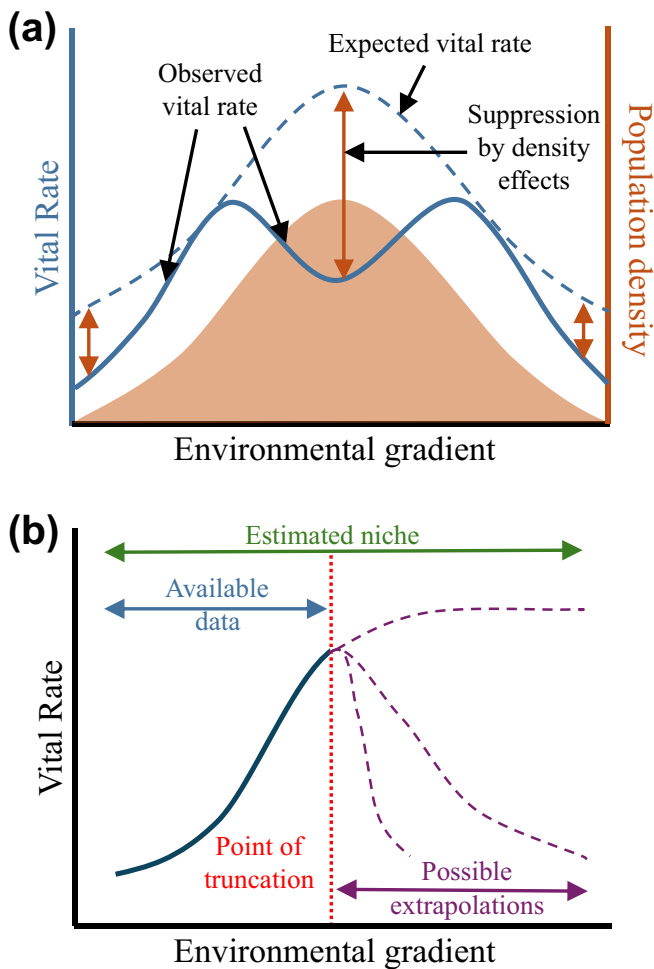


Figure 7. Deviations from a unimodal vital rate responses may stem from a range of biological and observation-bias factors. Two representative cases are presented here. (a) Vital rates are affected by density-dependent factors, resulting in suppressed vital rates at low and high population densities. The observed vital rate response thus deviates from a unimodal expectation, producing here a bimodal response. (b) Observed vital rate response may be truncated due to incomplete data or geographical limitations. The truncated response may be assumed to be the full, non-unimodal response. Alternatively, extrapolating the full response can be difficult and where unimodality can neither be confirmed nor rejected.

exhibit a ‘rugged landscape’ of multimodal responses due to complex interactions with other biological factors (Laughlin 2018). Rather than undermining the framework, such deviations can illuminate additional ecological and evolutionary processes that shape range-wide population dynamics.

Density-dependent effects

Vital rates may depart from unimodality due to Allee effects at low densities and negative density dependence at high densities (Stephens et al. 1999, Holden et al. 2021). Allee effects can suppress vital rates when populations are too sparse to allow effective reproduction or social interactions (Fig. 7a) (Lande 1998, Courchamp et al. 1999, Holt 2020b), while

high densities may reduce vital rates via increased competition for resources (Buckley et al. 2001) or pathogen risk (Janzen 1970, Connell 1971). Holt (2009) further noted the potential for organisms to both construct (Odling-Smee et al. 2003) and destroy their own niches (Klein 1968) at varying densities, mirroring the impact niche (how an organism impacts its environment) described by Chase and Leibold (2003). This dynamic was also illustrated by Maguire (1973, p. 222–224), who described how alga can deplete nutrients from the system until persistence is no longer possible. These effects can skew, flatten, or even create bimodal responses, particularly in transient zones with fluctuating densities such as range edges, colonisation fronts, or under dynamic contexts like biological invasions and climate change (Barraquand and Yoccoz 2013, Pironon et al. 2015, Dial et al. 2022, Fenollosa et al. 2025).

Demographic niche truncation

Even if vital rate responses are inherently unimodal, available or observable data may capture only part of that curve (Fig. 7b) (Bush et al. 2018, Peterson et al. 2018, Guisan et al. 2025). Such truncation of the demographic niche may arise from distributional disequilibrium (Svenning and Skov 2004, Rumpf et al. 2019, Willner et al. 2023, Pang et al. 2025), anthropogenic range contractions (Faurby and Araújo 2018, Rutrough et al. 2019, Pang et al. 2022), or biogeographical or dispersal limitations (Saupe et al. 2012, Bush et al. 2018, Chevalier et al. 2024); or more fundamentally, simply because vital rates are typically measured in persisting populations, where vital rates in environments associated with non-persistence are more difficult to observe and obtain. Asymmetrical responses (Hooper et al. 2008, Angilletta 2009, Amarasekare and Savage 2012) exacerbate the problem as missing data at the steep end makes accurate extrapolation of the full response near impossible without additional information. Truncated responses therefore risks painting an incomplete or misleading picture of the true pattern of vital rate variation.

Recognising these complications underscores the value of identifying where unimodal responses consistently hold: as benchmarks for interpreting deviations. For instance, invasive species may show unimodal patterns more often because of reduced biotic constraints (e.g. enemy release; Keane and Crawley 2002). Similarly, unimodality may apply most consistently to the dominant vital rate driving λ , as informed by life-history theory (Stearns 1992, Jensen 1996, Capdevila et al. 2022). Moreover, truncations may suggest hidden demographic responses that could become expressed under novel conditions, such as climate change (Bush et al. 2018, Chevalier et al. 2024). Thus, deviations from unimodality should be interpreted as informative signals of how real-world demography interacts with ecological and evolutionary context.

The road ahead

The demographic niche concept offers a powerful reframing of ecological niche theory – one grounded in both

environmental associations and the mechanistic underpinnings of species persistence. Emerging from Maguire's (1973) idea of 'biological responses', the DNC expands beyond occupancy to capture how organisms survive, grow, and reproduce across environmental space. Yet, like Maguire, our vision for the DNC is far broader. We imagine a multi-faceted niche structured by a constellation of biological responses including physiological rates (e.g. respiration and photosynthetic rates; Barker et al. 1997, Anthony and Connolly 2004), behavioural strategies (e.g. migration and dispersal; Smith and Stirling 1975, Zanden et al. 2013, Zurell 2017), and habitat modification (e.g. niche construction and destruction; Chase and Leibold 2003, Holt 2009). In this spirit, the DNC is not just an expansion – it is an invitation to progress towards a richer Hutchinsonian niche that integrates the demographic, behavioural, physiological, and interactional scaffolding that sustains life.

Recent theoretical developments deepen this vision. Biotic interactions like competition, predation, and mutualism structure species distributions but remain underexamined at the vital rate level, e.g. sapling versus adult survival (García-Cervigón et al. 2021, Kunstler et al. 2021). Capturing these processes at demographic resolution will be key to forecasting population responses to climate change (Coulson et al. 2001, 2011, Merow et al. 2017, Dial et al. 2022) and community reshuffling (Alexander et al. 2016, Esquivel-Muelbert et al. 2019, Antão et al. 2022). Emerging frameworks such as the interaction niche (Blüthgen et al. 2006, Dehling and Stouffer 2018, Dehling et al. 2022, Marjakangas et al. 2025) and trait-driven theories (McGill et al. 2006, Enquist et al. 2015, Larson and Funk 2016, Treurnicht et al. 2020, Buckley and Puy 2022) provide formal links between traits, network positions, and demographic outcomes. While rooted more closely to Eltonian or Grinnellian niche traditions (Grinnell 1904, Elton 1927, Soberón 2007, Dehling and Stouffer 2018), these developments advance a more dynamic and demographically explicit niche concept. Together, they reinforce that niches are not static entities defined solely by abiotic conditions, but instead emerge from a web of ecological interactions, trait-environment feedbacks, and evolutionary history.

A parallel frontier lies in disturbances. From fire-stimulated germination (Higgins et al. 2000) to light pollution disrupting phenology (Firebaugh and Haynes 2019), natural and anthropogenic disturbances can create transient demographic windows that enable or preclude persistence and shape niches and distributions (Bond and Midgley 2001, Wright et al. 2003, Pausas and Keeley 2014). Yet, disturbance remains an underdeveloped axis of niche theory. Recognising how disturbance regimes shape, shift, or erase demographic niches will be essential for understanding and predicting responses to global change and informing restoration and rewilding efforts (Hamilton and Burton 2023, Svenning et al. 2024, Pang et al. 2025).

Looking forward, although the DNC opens opportunities for more predictive, mechanistic ecology, empirical tractability remains a challenge. Unlike population models (typically temporal but site-limited) or SDMs (typically spatial but

time-agnostic), demographic niche models demand spatially and temporally structured data across life stages (Merow et al. 2014b, Evans et al. 2025). These demands are non-trivial; few species have sufficient coverage of vital rates across gradients and time periods. While pragmatic approaches offer a starting point (e.g. prioritizing key vital rates, assuming interdependencies), the optimal remains broad vital rate coverage across environmental gradients – ideally supplemented by experimental data (e.g. PlantPopNet initiative; Wardle and Buckley 2014).

However, this data challenge is increasingly surmountable. A growing number of studies have modelled demographic niches to varying degrees of complexity (Merow et al. 2014a, 2017, Pironon et al. 2018, Pagel et al. 2020, Holden et al. 2021, Carbeck et al. 2022, Dial et al. 2022), and demographic data availability is growing rapidly. Open-access MPM databases COMPADRE and COMADRE (Salguero-Gómez et al. 2015, 2016a) show exponential growths in species representation, with steadily rising numbers of species with three or more spatially distinct populations (Fig. 8). Additionally, ongoing initiatives, including the PADRINO (IPMs) database (Levin et al. 2022), NEON mammal datasets (NEON 2025), MASTREE+ database (Hackett-Pain et al. 2022), and Beauchamp's (2023) vertebrate survival data, continue to expand taxonomic and spatial reach. While only a handful of species could be modelled now, that is quickly changing. Now is the time to consolidate and expand demographic data collection efforts explicitly aimed at constructing demographic niche models, ensuring coverage across vital rates, life stages, and environmental gradients.

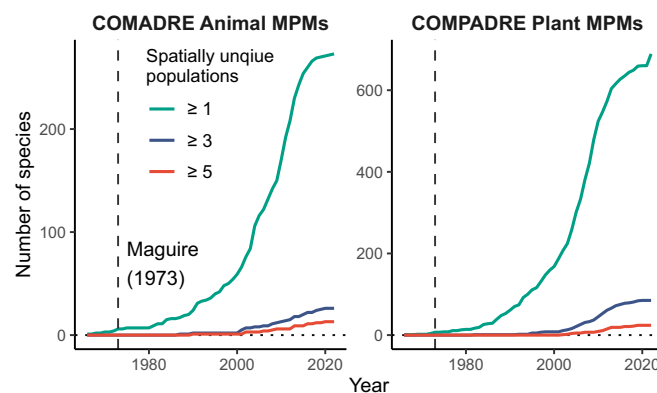


Figure 8. The exponential growth of spatial explicit demographic data over time from the COMADRE Animal (left panel) and COMPADRE Plant (right panel) MPM databases. The cumulative number of species (y-axis) with ≥ 1 (green), ≥ 3 (blue), and ≥ 5 (red) spatially unique populations, based on the year of data availability (x-axis) defined as the publication year. Populations were considered spatially unique if separated by at least 5 km, with thinning performed using the 'spThin' package in R (www.r-project.org, Aiello-Lammens et al. 2015) (Code availability). Unpublished records (COMADRE=0, COMPADRE=1) and populations without georeferencing (COMADRE=773, COMPADRE=998) were excluded. The dashed line marks the publication year of Maguire (1973).

Complementing these data gains are methodological advances. Missing vital rate relationships can be inferred using environmental covariates or population-level data (Merow et al. 2014a, Bernard et al. 2024), while missing vital rates can be imputed from phylogenetic relatives (James et al. 2021). The most transformative frontier perhaps lies in remote sensing: drones, LiDAR, and multispectral imagery now enable full IPM parameterization from survival, growth, and reproduction data across entire landscapes (Olsoy et al. 2024, Rosen et al. 2025). These tools move us from monitoring individuals in small plots to capturing demographic processes at scale – offering the capacity to observe everything, everywhere, all at once.

With theory in place and empirical pathways emerging, the DNC stands at a turning point. The DNC bridges ecological forecasting and biological realism, revealing not just where species occur, but also *why*, *how*, and *for how long*. The road ahead is to operationalize this framework: refining models, collecting targeted data, and building the next generation of tools and theory. In doing so, we edge closer to the dynamic, integrative niche Maguire envisioned – one that reflects the dynamic complexity behind life's persistence on Earth.

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We note with sadness the recent passing of Bassett Maguire Jr (1927–2025), whose inspiring 1973 paper laid the foundations for much of the work discussed in this review.

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Author contributions

Sean E. H. Pang: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Erola Fenollosa:** Writing – review and editing (equal). **Cory Merow:** Writing – review and editing (equal). **Antoine Guisan:** Writing – review and editing (equal). **Jens-Christian Svenning:** Writing – review and editing (equal). **Roberto Salguero-Gómez:** Conceptualization (supporting); Funding acquisition (supporting); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (equal).

Transparent peer review

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Data availability statement

There is no new data associated with this review article. Metadata from the COMADRE and COMPADRE database is publicly available at <https://compadre-db.org>.

Code used to simulate a hypothetical annual plant species and its vital rate variation, and to extract and prepare metadata from the COMPADRE and COMADRE databases are available at https://github.com/Pang-SEH/DN_C_review_2026.

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

References

- Åberg, P., Svensson, C. J., Caswell, H. and Pavia, H. 2009. Environment-specific elasticity and sensitivity analysis of the stochastic growth rate. – *Ecol. Modell.* 220: 605–610.
- Adler, P. B., Salguero-Gómez, R., Compagnoni, A., Hsu, J. S., Ray-Mukherjee, J., Mbeau-Ache, C. and Franco, M. 2014. Functional traits explain variation in plant life history strategies. – *Proc. Natl Acad. Sci. USA* 111: 740–745.
- Aiello-Lammens, M. E., Boria, R. A., Radosavljevic, A., Vilela, B. and Anderson, R. P. 2015. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. – *Ecography* 38: 541–545.
- Alexander, J. M., Diez, J. M., Hart, S. P. and Levine, J. M. 2016. When climate reshuffles competitors: a call for experimental macroecology. – *Trends Ecol. Evol.* 31: 831–841.
- Alexander, J. M., Chalmandrier, L., Lenoir, J., Burgess, T. I., Essl, F., Haider, S., Kueffer, C., McDougall, K., Milbau, A., Nuñez, M. A., Pauchard, A., Rabitsch, W., Rew, L. J., Sanders, N. J. and Pellissier, L. 2018. Lags in the response of mountain plant communities to climate change. – *Global Change Biol.* 24: 563–579.
- Amarasekare, P. and Nisbet, R. M. 2001. Spatial heterogeneity, source-sink dynamics, and the local coexistence of competing species. – *Am. Nat.* 158: 572–584.
- Amarasekare, P. and Savage, V. 2012. A framework for elucidating the temperature dependence of fitness. – *Am. Nat.* 179: 178–191.
- Anderegg, W. R., Kane, J. M. and Anderegg, L. D. 2013. Consequences of widespread tree mortality triggered by drought and temperature stress. – *Nat. Clim. Change* 3: 30.
- Anderson, R. P. 2017. When and how should biotic interactions be considered in models of species niches and distributions? – *J. Biogeogr.* 44: 8–17.
- Angilletta, M. J. 2009. Thermal adaptation: a theoretical and empirical synthesis. – Oxford Univ. Press.
- Antão, L. H. et al. 2022. Climate change reshuffles northern species within their niches. – *Nat. Clim. Change* 12: 587–592.
- Anthony, K. R. N. and Connolly, S. R. 2004. Environmental limits to growth: physiological niche boundaries of corals along turbidity–light gradients. – *Oecologia* 141: 373–384.
- Anujan, K., McMahan, S. M., Bunyavejchewin, S., Davies, S. J., Muller-Landau, H. C., Pongpattananurak, N. and Anderson-Teixeira, K. J. 2026. Drought response is not a species trait: tropical tree drought sensitivity is shaped by drought characteristics, species adaptations and individual microenvironments. – *Ecol. Lett.* 29: e70291.

- Araújo, M. B. and Luoto, M. 2007. The importance of biotic interactions for modelling species distributions under climate change. – *Global Ecol. Biogeogr.* 16: 743–753.
- Araújo, R. M., Serrão, E. A., Sousa-Pinto, I. and Åberg, P. 2014. Spatial and temporal dynamics of fucoid populations (*Ascophyllum nodosum* and *Fucus serratus*): a comparison between central and range edge populations. – *PLoS One* 9: e92177.
- Arft, A. M. et al. 1999. Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. – *Ecol. Monogr.* 69: 491–511.
- Ashton, P. S., Givnish, T. J. and Appanah, S. 1988. Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the Aseasonal tropics. – *Am. Nat.* 132: 44–66.
- Austin, M. P. 1985. Continuum concept, ordination methods, and niche theory. – *Annu. Rev. Ecol. Syst.* 16: 39–61.
- Austin, M. 2007. Species distribution models and ecological theory: a critical assessment and some possible new approaches. – *Ecol. Modell.* 200: 1–19.
- Bajocco, S., Ferrara, C., Bascietto, M., Alivernini, A., Chirichella, R., Cutini, A. and Chianucci, F. 2021. Characterizing the climatic niche of mast seeding in beech: evidences of trade-offs between vegetation growth and seed production. – *Ecol. Indic.* 121: 107139.
- Barker, M. G., Press, M. C. and Brown, N. D. 1997. Photosynthetic characteristics of dipterocarp seedlings in three tropical rain forest light environments: a basis for niche partitioning? – *Oecologia* 112: 453–463.
- Barraquand, F. and Yoccoz, N. G. 2013. When can environmental variability benefit population growth? Counterintuitive effects of nonlinearities in vital rates. – *Theor. Popul. Biol.* 89: 1–11.
- Barthold, J. A., Loveridge, A. J., Macdonald, D. W., Packer, C. and Colchero, F. 2016. Bayesian estimates of male and female African lion mortality for future use in population management. – *J. Appl. Ecol.* 53: 295–304.
- Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S. P., Peterson, A. T., Soberón, J. and Villalobos, F. 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. – *Ecology* 222: 1810–1819.
- Bateman, B. L., Murphy, H. T., Reside, A. E., Mokany, K. and VanDerWal, J. 2013. Appropriateness of full-, partial- and no-dispersal scenarios in climate change impact modelling. – *Divers. Distrib.* 19: 1224–1234.
- Bauman, D., Fortunel, C., Delhaye, G., Malhi, Y., Cernusak, L. A., Bentley, L. P., Rifai, S. W., Aguirre-Gutiérrez, J., Menor, I. O., Phillips, O. L., McNellis, B. E., Bradford, M., Laurance, S. G. W., Hutchinson, M. F., Dempsey, R., Santos-Andrade, P. E., Ninantay-Rivera, H. R., Chambi Paucar, J. R. and McMahon, S. M. 2022. Tropical tree mortality has increased with rising atmospheric water stress. – *Nature* 608: 528–533.
- Beauchamp, G. 2023. Annual apparent survival across species is lower in juvenile than adult birds but has similar ecological correlates. – *Ibis* 165: 448–457.
- Benito Garzón, M., Robson, T. M. and Hampe, A. 2019. Δ Trait SDMs : species distribution models that account for local adaptation and phenotypic plasticity. – *New Phytol.* 222: 1757–1765.
- Bernard, C. D., Bonsall, M. B. and Salguero-Gómez, R. 2024. Life histories and study duration matter less than prior knowledge of vital rates to inverse integral projection models. – *bioRxiv* doi: [10.1101/2024.04.06.588423](https://doi.org/10.1101/2024.04.06.588423).
- Blonder, B., Lamanna, C., Violle, C. and Enquist, B. J. 2014. The n -dimensional hypervolume: the n -dimensional hypervolume. – *Global Ecol. Biogeogr.* 23: 595–609.
- Blüthgen, N., Menzel, F. and Blüthgen, N. 2006. Measuring specialization in species interaction networks. – *BMC Ecol.* 6: 9.
- Bond, W. J. and Midgley, J. J. 2001. Ecology of sprouting in woody plants: the persistence niche. – *Trends Ecol. Evol.* 16: 45–51.
- Boyce, M. S. 1977. Population growth with stochastic fluctuations in the life table. – *Theor. Popul. Biol.* 12: 366–373.
- Briscoe, N. J., Elith, J., Salguero-Gómez, R., Lahoz-Monfort, J. J., Camac, J. S., Giljohann, K. M., Holden, M. H., Hradsky, B. A., Kearney, M. R., McMahon, S. M., Phillips, B. L., Regan, T. J., Rhodes, J. R., Vesik, P. A., Wintle, B. A., Yen, J. D. L. and Guillera-Arroita, G. 2019. Forecasting species range dynamics with process-explicit models: matching methods to applications. – *Ecol. Lett.* 22: 1940–1956.
- Briscoe, N. J., Morris, S. D., Mathewson, P. D., Buckley, L. B., Jusup, M., Levy, O., Maclean, I. M. D., Pincebourde, S., Riddell, E. A., Roberts, J. A., Schouten, R., Sears, M. W. and Kearney, M. R. 2023. Mechanistic forecasts of species responses to climate change: the promise of biophysical ecology. – *Global Change Biol.* 29: 1451–1470.
- Broennimann, O., Petitpierre, B., Chevalier, M., González-Suárez, M., Jeschke, J. M., Rolland, J., Gray, S. M., Bacher, S. and Guisan, A. 2021. Distance to native climatic niche margins explains establishment success of alien mammals. – *Nat. Commun.* 12: 2353.
- Brokaw, N. V. L. 1985. Gap-phase regeneration in a tropical forest. – *Ecology* 66: 682–687.
- Brown, J. H. 1984. On the relationship between abundance and distribution of species. – *Am. Nat.* 124: 255–279.
- Buckley, Y. M. and Puy, J. 2022. The macroecology of plant populations from local to global scales. – *New Phytol.* 233: 1038–1050.
- Buckley, Y. M., Hinz, H. L., Matthies, D. and Rees, M. 2001. Interactions between density-dependent processes, population dynamics and control of an invasive plant species, *Tripleurospermum perforatum* (scentless chamomile). – *Ecol. Lett.* 4: 551–558.
- Bush, A., Catullo, R. A., Mokany, K., Thornhill, A. H., Miller, J. T. and Ferrier, S. 2018. Truncation of thermal tolerance niches among Australian plants. – *Global Ecol. Biogeogr.* 27: 22–31.
- Bykova, O., Chuine, I., Morin, X. and Higgins, S. I. 2012. Temperature dependence of the reproduction niche and its relevance for plant species distributions. – *J. Biogeogr.* 39: 2191–2200.
- Capdevila, P., Stott, I., Cant, J., Beger, M., Rowlands, G., Grace, M. and Salguero-Gómez, R. 2022. Life history mediates the trade-offs among different components of demographic resilience. – *Ecol. Lett.* 25: 1566–1579.
- Carbeck, K., Wang, T., Reid, J. M. and Arcese, P. 2022. Adaptation to climate change through seasonal migration revealed by climatic versus demographic niche models. – *Global Change Biol.* 28: 4260–4275.
- Carley, L. N., Geber, M. A., Morris, W. F., Eckhart, V. M. and Moeller, D. A. 2025. Local adaptation is highest in populations with stable long-term growth. – *Ecol. Lett.* 28: e70071.
- Carlson, B. Z., Randin, C. F., Boulangeat, I., Lavergne, S., Thuiller, W. and Choler, P. 2013. Working toward integrated models of alpine plant distribution. – *Alp. Bot.* 123: 41–53.
- Carscadden, K. A., Emery, N. C., Arnillas, C. A., Cadotte, M. W., Afkhami, M. E., Gravel, D., Livingstone, S. W. and Wiens, J. J. 2020. Niche breadth: causes and consequences for ecology, evolution, and conservation. – *Q. Rev. Biol.* 95: 179–214.
- Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation, 2nd edn. – Sinauer Associates.
- Caswell, H. 2005. Sensitivity analysis of the stochastic growth rate: three extensions. – *Aust. N. Z. J. Stat.* 47: 75–85.

- Caswell, H. 2010. Life table response experiment analysis of the stochastic growth rate. – *J. Ecol.* 98: 324–333.
- Caughley, G. 1994. Directions in conservation biology. – *J. Anim. Ecol.* 63: 215.
- Chapin III, F. S. and Shaver, G. R. 1996. Physiological and growth responses of arctic plants to a field experiment simulating climatic change. – *Ecology* 77: 822–840.
- Chapman, D. S., Scalone, R., Štefanić, E. and Bullock, J. M. 2017. Mechanistic species distribution modeling reveals a niche shift during invasion. – *Ecology* 98: 1671–1680.
- Chardon, N. I., Pironon, S., Peterson, M. L. and Doak, D. F. 2020. Incorporating intraspecific variation into species distribution models improves distribution predictions, but cannot predict species traits for a wide-spread plant species. – *Ecography* 43: 60–74.
- Chase, J. M. and Leibold, M. A. 2003. Ecological niches: linking classical and contemporary approaches. – Univ. of Chicago Press.
- Chevalier, M., Broennimann, O. and Guisan, A. 2021. Using a robust multi-settings inference framework on published datasets still reveals limited support for the abundant centre hypothesis: more testing needed on other datasets. – *Global Ecol. Biogeogr.* 30: 2211–2228.
- Chevalier, M., Broennimann, O. and Guisan, A. 2024. Climate change may reveal currently unavailable parts of species' ecological niches. – *Nat. Ecol. Evol.* 8: 1298–1310.
- Chisholm, R. A. et al. 2024. Assessing the spatial scale of synchrony in forest tree population dynamics. – *Proc. R. Soc. B* 291: 20240486.
- Citres, L., Ibaibarriaga, L., Lee, D.-J., Brewer, M. J., Santos, M. and Chust, G. 2020. Modelling species presence–absence in the ecological niche theory framework using shape-constrained generalized additive models. – *Ecol. Modell.* 418: 108926.
- Colwell, R. K. and Rangel, T. F. 2009. Hutchinson's duality: the once and future niche. – *Proc. Natl Acad. Sci. USA* 106: 19651–19658.
- Condit, R. et al. 2006. The importance of demographic niches to tree diversity. – *Science* 313: 98–101.
- Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. – *Dyn. Popul.* 298: 298–312.
- Cook, W. C. 1929. A bioclimatic zonation for studying the economic distribution of injurious insects. – *Ecology* 10: 282–293.
- Cook, W. C. 1931. Notes on predicting the probable future distribution of introduced insects. – *Ecology* 12: 245–247.
- Corlett, R. T. and Tomlinson, K. W. 2020. Climate change and edaphic specialists: irresistible force meets immovable object? – *Trends Ecol. Evol.* 35: 367–376.
- Coulson, T., Catchpole, E. A., Albon, S. D., Morgan, B. J. T., Pemberton, J. M., Clutton-Brock, T. H., Crawley, M. J. and Grenfell, B. T. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. – *Science* 292: 1528–1531.
- Coulson, T., MacNulty, D. R., Stahler, D. R., vonHoldt, B., Wayne, R. K. and Smith, D. W. 2011. Modeling effects of environmental change on wolf population dynamics, trait evolution, and life history. – *Science* 334: 1275–1278.
- Courchamp, F., Clutton-Brock, T. and Grenfell, B. 1999. Inverse density dependence and the Allee effect. – *Trends Ecol. Evol.* 14: 405–410.
- Crozier, L. and Dwyer, G. 2006. Combining population-dynamic and ecophysiological models to predict climate-induced insect Range shifts. – *Am. Nat.* 167: 853–866.
- Csergő, A. M., Salguero-Gómez, R., Broennimann, O., Coutts, S. R., Guisan, A., Angert, A. L., Welk, E., Stott, I., Enquist, B. J., McGill, B., Svenning, J. C., Violle, C. and Buckley, Y. M. 2017. Less favourable climates constrain demographic strategies in plants. – *Ecol. Lett.* 20: 969–980.
- Dahlgren, J. P. and Ehrlén, J. 2009. Linking environmental variation to population dynamics of a forest herb. – *J. Ecol.* 97: 666–674.
- Dallas, T., Decker, R. R. and Hastings, A. 2017. Species are not most abundant in the centre of their geographic range or climatic niche. – *Ecol. Lett.* 20: 1526–1533.
- de Kroon, H., Plaisier, A., van Groenendael, J. and Caswell, H. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. – *Ecology* 67: 1427–1431.
- de Kroon, H., van Groenendael, J. and Ehrlén, J. 2000. Elasticities: a review of methods and model limitations. – *Ecology* 81: 607–618.
- DeAngelis, D. L. and Mooij, W. M. 2005. Individual-based modeling of ecological and evolutionary processes. – *Annu. Rev. Ecol. Evol. Syst.* 36: 147–168.
- Dehling, D. M. and Stouffer, D. B. 2018. Bringing the Eltonian niche into functional diversity. – *Oikos* 127: 1711–1723.
- Dehling, D. M., Barreto, E. and Graham, C. H. 2022. The contribution of mutualistic interactions to functional and phylogenetic diversity. – *Trends Ecol. Evol.* 37: 768–776.
- Denslow, J. S. 1987. Tropical rainforest gaps and tree species diversity. – *Annu. Rev. Ecol. Syst.* 18: 431–451.
- Dial, R. J., Maher, C. T., Hewitt, R. E. and Sullivan, P. F. 2022. Sufficient conditions for rapid range expansion of a boreal conifer. – *Nature* 608: 546–551.
- Díaz, S. et al. 2016. The global spectrum of plant form and function. – *Nature* 529: 167–171.
- Doak, D. F. and Morris, W. F. 2010. Demographic compensation and tipping points in climate-induced range shifts. – *Nature* 467: 959–962.
- Dormann, C. F. 2007. Promising the future? Global change projections of species distributions. – *Basic Appl. Ecol.* 8: 387–397.
- Dormann, C. F., Schymanski, S. J., Cabral, J., Chuine, I., Graham, C., Hartig, F., Kearney, M., Morin, X., Römermann, C., Schröder, B. and Singer, A. 2012. Correlation and process in species distribution models: bridging a dichotomy. – *J. Biogeogr.* 39: 2119–2131.
- Dormann, C. F., Bobrowski, M., Dehling, D. M., Harris, D. J., Hartig, F., Lischke, H., Moretti, M. D., Pagel, J., Pinkert, S., Schleuning, M., Schmidt, S. I., Sheppard, C. S., Steinbauer, M. J., Zeuss, D. and Kraan, C. 2018. Biotic interactions in species distribution modelling: 10 questions to guide interpretation and avoid false conclusions. – *Global Ecol. Biogeogr.* 27: 1004–1016.
- Drake, J. M. 2015. Range bagging: a new method for ecological niche modelling from presence-only data. – *J. R. Soc. Interface* 12: 20150086.
- Dullinger, S. et al. 2012. Extinction debt of high-mountain plants under twenty-first-century climate change. – *Nat. Clim. Change* 2: 619–622.
- Easterling, M. R., Ellner, S. P. and Dixon, P. M. 2000. Size-specific sensitivity: applying a new structured population model. – *Ecology* 81: 694–708.
- Ebert, T. 1999. Plant and animal populations. Methods in demography. – Academic Press.

- Ehrlén, J. and Morris, W. F. 2015. Predicting changes in the distribution and abundance of species under environmental change. – *Ecol. Lett.* 18: 303–314.
- Ehrlén, J., Morris, W. F., Euler, T. and Dahlgren, J. P. 2016. Advancing environmentally explicit structured population models of plants. – *J. Ecol.* 104: 292–305.
- Ellith, J. and Leathwick, J. R. 2009. Species distribution models: ecological explanation and prediction across space and time. – *Annu. Rev. Ecol. Evol. Syst.* 40: 677–697.
- Ellison, A. M. 2004. Bayesian inference in ecology. – *Ecol. Lett.* 7: 509–520.
- Ellner, S. P. and Rees, M. 2006. Integral projection models for species with complex demography. – *Am. Nat.* 167: 410–428.
- Elton, C. S. 1927. *Animal ecology*. – Univ. of Chicago Press.
- Enquist, B. J., Norberg, J., Bonser, S. P., Violle, C., Webb, C. T., Henderson, A., Sloat, L. L. and Savage, V. M. 2015. Scaling from traits to ecosystems: developing a general trait driver theory via integrating trait-based and metabolic scaling theories. – In: Pawar, S. et al. (eds), *Advances in ecological research. Trait-based ecology – from structure to function*. Academic Press, pp. 249–318.
- Erguler, K., Mendel, J., Petrić, D. V., Petrić, M., Kavran, M., Demirok, M. C., Gunay, F., Georgiades, P., Alten, B. and Lelieveld, J. 2022. A dynamically structured matrix population model for insect life histories observed under variable environmental conditions. – *Sci. Rep.* 12: 11587.
- Espelta, J. M., Cortés, P., Molowny-Horas, R., Sánchez-Humanes, B. and Retana, J. 2008. Masting mediated by summer drought reduces acorn predation in Mediterranean oak forests. – *Ecology* 89: 805–817.
- Esquivel-Muelbert, A., et al. 2019. Compositional response of Amazon forests to climate change. – *Global Change Biol.* 25: 39–56.
- Evans, M. E. K., Merow, C., Record, S., McMahon, S. M. and Enquist, B. J. 2016. Towards process-based Range modeling of many species. – *Trends Ecol. Evol.* 31: 860–871.
- Evans, M. E. K., Adler, P. B., Angert, A. L., Dey, S. M. N., Girardin, M. P., Heilman, K. A., Klesse, S., Perret, D. L., Sax, D. F., Sheth, S. N., Stenkovski, M. and Williams, J. L. 2025. Reconsidering space-for-time substitution in climate change ecology. – *Nat. Clim. Change* 15: 809–812.
- Ezard, T. H. G., Bullock, J. M., Dalgleish, H. J., Millon, A., Pelletier, F., Ozgul, A. and Koons, D. N. 2010. Matrix models for a changeable world: the importance of transient dynamics in population management: transient dynamics and population management. – *J. Appl. Ecol.* 47: 515–523.
- Farquhar, G. D., Von Caemmerer, S. and Berry, J. A. 1980. A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species. – *Planta* 149: 78–90.
- Faurby, S. and Araújo, M. B. 2018. Anthropogenic range contractions bias species climate change forecasts. – *Nat. Clim. Change* 8: 252–256.
- Fenollosa, E., Pang, S. E. H., Briscoe, N. J., Guisan, A. and Salguero-Gómez, R. 2025. Powerful yet challenging: mechanistic niche models for predicting invasive species potential distribution under climate change. – *Ecography* 2025: e07775.
- Firebaugh, A. and Haynes, K. J. 2019. Light pollution may create demographic traps for nocturnal insects. – *Basic Appl. Ecol.* 34: 118–125.
- Foest, J. J., Szymkowiak, J., Dyderski, M. K., Jastrzębowski, S., Fuchs, H., Ratajczak, E., Hacket-Pain, A. and Bogdziewicz, M. 2025. No refuge at the edge for European beech as climate warming disproportionately reduces masting at colder margins. – *Ecol. Lett.* 28: e70284.
- Franco, M. and Silvertown, J. 2004. A comparative demography of plants based upon elasticities of vital rates. – *Ecology* 85: 531–538.
- Fréville, H. and Silvertown, J. 2005. Analysis of interspecific competition in perennial plants using Life Table Response Experiments. – *Plant Ecol.* 176: 69–78.
- García-Cervigón, A. I., Quintana-Ascencio, P. F., Escudero, A., Ferrer-Cervantes, M. E., Sánchez, A. M., Iriondo, J. M. and Olano, J. M. 2021. Demographic effects of interacting species: exploring stable coexistence under increased climatic variability in a semiarid shrub community. – *Sci Rep* 11: 3099.
- Gibson, L., Lynam, A. J., Bradshaw, C. J. A., He, F., Bickford, D. P., Woodruff, D. S., Bumrungsri, S. and Laurance, W. F. 2013. Near-complete extinction of native small mammal fauna 25 years after forest fragmentation. – *Science* 341: 1508–1510.
- Godsoe, W., Franklin, J. and Blanchet, F. G. 2017. Effects of biotic interactions on modeled species' distribution can be masked by environmental gradients. – *Ecol. Evol.* 7: 654–664.
- Green, R. H. 1971. A multivariate statistical approach to the Hutchinsonian niche: bivalve molluscs of central Canada. – *Ecology* 52: 543–556.
- Grime, J. P. 2006. *Plant strategies, vegetation processes, and ecosystem properties*. – Wiley.
- Grimm, V., Ayllón, D. and Railsback, S. F. 2017. Next-generation individual-based models integrate biodiversity and ecosystems: yes we can, and yes we must. – *Ecosystems* 20: 229–236.
- Grinnell, J. 1904. The origin and distribution of the chest-nut-backed chickadee. – *Auk* 21: 364–382.
- Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. – *Biol. Rev.* 52: 107–145.
- Guevara, L., Gerstner, B. E., Kass, J. M. and Anderson, R. P. 2018. Toward ecologically realistic predictions of species distributions: a cross-time example from tropical montane cloud forests. – *Global Change Biol.* 24: 1511–1522.
- Guisan, A. et al. 2013. Predicting species distributions for conservation decisions. – *Ecol. Lett.* 16: 1424–1435.
- Guisan, A., Petitpierre, B., Broennimann, O., Daehler, C. and Kueffer, C. 2014. Unifying niche shift studies: insights from biological invasions. – *Trends Ecol. Evol.* 29: 260–269.
- Guisan, A., Thuiller, W. and Zimmermann, N. E. 2017. *Habitat suitability and distribution models: with applications in R*. – Cambridge Univ. Press.
- Guisan, A., Chevalier, M., Adde, A., Zarzo-Arias, A., Goicolea, T., Broennimann, O., Petitpierre, B., Scherrer, D., Rey, P.-L., Col-lart, F., Riva, F., Steen, B. and Mateo, R. G. 2025. Spatially nested species distribution models (N-SDM): an effective tool to overcome niche truncation for more robust inference and projections. – *J. Ecol.* 113: 1588–1605.
- Hacket-Pain, A., et al. 2022. MASTREE+: time-series of plant reproductive effort from six continents. – *Global Change Biol.* 28: 3066–3082.
- Hageer, Y., Esperón-Rodríguez, M., Baumgartner, J. B. and Beaumont, L. J. 2017. Climate, soil or both? Which variables are better predictors of the distributions of Australian shrub species? – *PeerJ* 5: e3446.
- Hamilton, N. P. and Burton, P. J. 2023. Wildfire disturbance reveals evidence of ecosystem resilience and precariousness in a forest–grassland mosaic. – *Ecosphere* 14: e4460.

- Hanski, I. 1998. Metapopulation dynamics. – *Nature* 396: 41–49.
- Harpole, W. S., Ngai, J. T., Cleland, E. E., Seabloom, E. W., Borer, E. T., Bracken, M. E. S., Elser, J. J., Gruner, D. S., Hillebrand, H., Shurin, J. B. and Smith, J. E. 2011. Nutrient co-limitation of primary producer communities. – *Ecol. Lett.* 14: 852–862.
- Healy, K., Ezard, T. H. G., Jones, O. R., Salguero-Gómez, R. and Buckley, Y. M. 2019. Animal life history is shaped by the pace of life and the distribution of age-specific mortality and reproduction. – *Nat. Ecol. Evol.* 3: 1217–1224.
- Heiland, L., Kunstler, G., Ruiz-Benito, P., Buras, A., Dahlgren, J. and Hülsmann, L. 2022. Divergent occurrences of juvenile and adult trees are explained by both environmental change and ontogenetic effects. – *Ecography* 2022: e06042.
- Heppell, S. S. 1998. Application of life-history theory and population model analysis to turtle conservation. – *Copeia* 1998: 367–375.
- Herfindal, I., van de Pol, M., Nielsen, J. T., Saether, B.-E. and Møller, A. P. 2015. Climatic conditions cause complex patterns of covariation between demographic traits in a long-lived raptor. – *J. Anim. Ecol.* 84: 702–711.
- Hernández, C. M., Ellner, S. P., Adler, P. B., Hooker, G. and Snyder, R. E. 2023. An exact version of Life Table Response Experiment analysis, and the R package exactLTRE. – *Methods Ecol. Evol.* 14: 939–951.
- Higgins, S. I., Bond, W. J. and Trollope, W. S. W. 2000. Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. – *J. Ecol.* 88: 213–229.
- Higgins, S. I., Larcombe, M. J., Beeton, N. J., Conradi, T. and Nottebrock, H. 2020. Predictive ability of a process-based versus a correlative species distribution model. – *Ecol. Evol.* 10: 11043–11054.
- Hilde, C. H., Gamelon, M., Sæther, B.-E., Gaillard, J.-M., Yoccoz, N. G. and Pélabon, C. 2020. The demographic buffering hypothesis: evidence and challenges. – *Trends Ecol. Evol.* 35: 523–538.
- Holden, M. H., Yen, J. D. L., Briscoe, N. J., Lahoz-Monfort, J. J., Salguero-Gómez, R., Veski, P. A. and Guillerá-Arroita, G. 2021. Assessing the accuracy of density-independent demographic models for predicting species ranges. – *Ecography* 44: 345–357.
- Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. – *Can. Entomol.* 91: 385–398.
- Holt, R. D. 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. – *Proc. Natl Acad. Sci. USA* 106: 19659–19665.
- Holt, R. D. 2020a. Some thoughts about the challenge of inferring ecological interactions from spatial data. – *Biodiv. Inform.* 15: 61–66.
- Holt, R. D. 2020b. Reflections on niches and numbers. – *Ecography* 43: 387–390.
- Hooper, H. L., Connon, R., Callaghan, A., Fryer, G., Yarwood-Buchanan, S., Biggs, J., Maund, S. J., Hutchinson, T. H. and Sibly, R. M. 2008. The ecological niche of *daphnia magna* characterized using population growth rate. – *Ecology* 89: 1015–1022.
- Howe, H. F. and Smallwood, J. 1982. Ecology of seed dispersal. – *Annu. Rev. Ecol. Syst.* 13: 201–228.
- Hutchinson, G. E. 1957. Concluding remarks. – *Cold Spring Harb. Symp. Quant. Biol.* 22: 415–427.
- Hutchinson, G. E. 1978. An introduction to population ecology. – Yale Univ. Press.
- Iles, D. T., Rockwell, R. F. and Koons, D. N. 2019. Shifting vital rate correlations alter predicted population responses to increasingly variable environments. – *Am. Nat.* 193: E57–E64.
- Iverson, L. R. and McKenzie, D. 2013. Tree-species range shifts in a changing climate: detecting, modeling, assisting. – *Landsc. Ecol.* 28: 879–889.
- James, T. D., Salguero-Gómez, R., Jones, O. R., Childs, D. Z. and Beckerman, A. P. 2021. Bridging gaps in demographic analysis with phylogenetic imputation. – *Conserv. Biol.* 35: 1210–1221.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. – *Am. Nat.* 104: 501–528.
- Jensen, A. L. 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. – *Can. J. Fish. Aquat. Sci.* 53: 820–822.
- Keane, R. M. and Crawley, M. J. 2002. Exotic plant invasions and the enemy release hypothesis. – *Trends Ecol. Evol.* 17: 164–170.
- Kelly, D. and Sork, V. L. 2002. Mast seeding in perennial plants: why, how, where? – *Annu. Rev. Ecol. Syst.* 33: 427–447.
- Kitajima, K. and Poorter, L. 2008. Functional basis for resource niche partitioning by tropical trees. – *Trop. For. Commun. Ecol.* 1936: 160–181.
- Klein, D. R. 1968. The introduction, increase, and crash of reindeer on St. Matthew island. – *J. Wildl. Manage.* 32: 350.
- Kobe, R. K. 1999. Light gradient partitioning among tropical tree species through differential seedling mortality and growth. – *Ecology* 80: 187–201.
- Koenig, W. D., Alejano, R., Carbonero, M. D., Fernández-Rebollo, P., Knops, J. M. H., Marañón, T., Padilla-Díaz, C. M., Pearse, I. S., Pérez-Ramos, I. M., Vázquez-Piqué, J. and Pendorfer, M. B. 2016. Is the relationship between mast-seeding and weather in oaks related to their life-history or phylogeny? – *Ecology* 97: 2603–2615.
- Kunstler, G., Guyennon, A., Ratcliffe, S., Rüger, N., Ruiz-Benito, P., Childs, D. Z., Dahlgren, J., Lehtonen, A., Thuiller, W., Wirth, C., Zavala, M. A. and Salguero-Gomez, R. 2021. Demographic performance of European tree species at their hot and cold climatic edges. – *J. Ecol.* 109: 1041–1054.
- Lalechère, E., Marrec, R. and Lenoir, J. 2025. A non-equilibrium species distribution model reveals unprecedented depth of time lag responses to past environmental change trajectories. – *Ecol. Lett.* 28: e70040.
- Lambers, H. and Oliveira, R. S. 2019. Life cycles: environmental influences and adaptations. – In: Lambers, H. and Oliveira, R. S. (eds), *Plant physiological ecology*. Springer International Publishing, pp. 451–486.
- Lande, R. 1998. Demographic stochasticity and allee effect on a scale with isotropic noise. – *Oikos* 83: 353–358.
- Larson, J. E. and Funk, J. L. 2016. Regeneration: an overlooked aspect of trait-based plant community assembly models. – *J. Ecol.* 104: 1284–1298.
- Larson, J. E., Agneray, A. C., Boyd, C. S., Bradford, J. B., Kildisheva, O. A., Suding, K. N. and Copeland, S. M. 2023. A recruitment niche framework for improving seed-based restoration. – *Restor. Ecol.* 31: e13959.
- Laughlin, D. C. 2018. Rugged fitness landscapes and Darwinian demons in trait-based ecology. – *New Phytol.* 217: 501–503.
- Lee-Yaw, J. A., McCune, L., Pironon, S. and Sheth, N. 2022. Species distribution models rarely predict the biology of real populations. – *Ecography* 2022: e05877.
- Levin, S. C., Childs, D. Z., Compagnoni, A., Evers, S., Knight, T. M. and Salguero-Gómez, R. 2021. ipmr: flexible implementation of Integral Projection Models in R. – *Methods Ecol. Evol.* 12: 1826–1834.

- Levin, S. C., Evers, S., Potter, T., Guerrero, M. P., Childs, D. Z., Compagnoni, A., Knight, T. M. and Salguero-Gómez, R. 2022. Rpadrino: an R package to access and use PADRINO, an open access database of integral projection models. – *Methods Ecol. Evol.* 13: 1923–1929.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. – *Bull. Entomol. Soc. Am.* 15: 237–240.
- Liebig, J. F. 1840. *Die organische Chemie in ihrer Anwendung auf Agricultur und Physiologie* (Organic chemistry in its applications to agriculture and physiology). – F. Vieweg.
- Liu, C., Newell, G. and White, M. 2016. On the selection of thresholds for predicting species occurrence with presence-only data. – *Ecol. Evol.* 6: 337–348.
- Liu, H., Ye, Q. and Wiens, J. J. 2020. Climatic-niche evolution follows similar rules in plants and animals. – *Nat. Ecol. Evol.* 4: 753–763.
- Machado-Stredel, F., Cobos, M. E. and Peterson, A. T. 2021. A simulation-based method for selecting calibration areas for ecological niche models and species distribution models. – *Front. Biogeogr.* 13: e48814.
- Maguire, B. 1973. Niche response structure and the analytical potentials of its relationship to the habitat. – *Am. Nat.* 107: 213–246.
- Måren, I. E. and Vandvik, V. 2009. Fire and regeneration: the role of seed banks in the dynamics of northern heathlands. – *J. Veg. Sci.* 20: 871–888.
- Marjakangas, E.-L., Dalsgaard, B. and Ordonez, A. 2025. Fundamental interaction niches: towards a functional understanding of ecological networks' resilience. – *Ecol. Lett.* 28: e70146.
- Martínez-Meyer, E., Díaz-Porrás, D., Peterson, A. T. and Yáñez-Arenas, C. 2013. Ecological niche structure and rangewide abundance patterns of species. – *Biol. Lett.* 9: 20120637.
- Maxwell, S. L., Fuller, R. A., Brooks, T. M. and Watson, J. E. M. 2016. Biodiversity: the ravages of guns, nets and bulldozers. – *Nature* 536: 143–145.
- McDonald, J. L., Stott, I., Townley, S. and Hodgson, D. J. 2016. Transients drive the demographic dynamics of plant populations in variable environments. – *J. Ecol.* 104: 306–314.
- McGill, B. J., Enquist, B. J., Weiher, E. and Westoby, M. 2006. Rebuilding community ecology from functional traits. – *Trends Ecol. Evol.* 21: 178–185.
- Merow, C., Smith, M. J. and Silander, J. A. 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. – *Ecography* 36: 1058–1069.
- Merow, C., Latimer, A. M., Wilson, A. M., McMahon, S. M., Rebelo, A. G. and Silander, J. A. 2014a. On using integral projection models to generate demographically driven predictions of species' distributions: development and validation using sparse data. – *Ecography* 37: 1167–1183.
- Merow, C., Dahlgren, J. P., Metcalf, C. J. E., Childs, D. Z., Evans, M. E. K., Jongejans, E., Record, S., Rees, M., Salguero-Gómez, R. and McMahon, S. M. 2014b. Advancing population ecology with integral projection models: a practical guide. – *Methods Ecol. Evol.* 5: 99–110.
- Merow, C., Bois, S. T., Allen, J. M., Xie, Y. and Silander, J. A. 2017. Climate change both facilitates and inhibits invasive plant ranges in New England. – *Proc. Natl Acad. Sci. USA* 114: E3276–E3284.
- Metcalf, C. J. E. 2016. Invisible trade-offs: Van Noordwijk and de Jong and life-history evolution. – *Am. Nat.* 187: iii–v.
- Metcalf, C. J. E., McMahon, S. M., Salguero-Gómez, R. and Jongejans, E. 2013. IPM pack: an R package for integral projection models. – *Methods Ecol. Evol.* 4: 195–200.
- Morales, N. S., Fernández, I. C. and Baca-González, V. 2017. MaxEnt's parameter configuration and small samples: are we paying attention to recommendations? A systematic review. – *PeerJ* 5: e3093.
- Morin, X. and Thuiller, W. 2009. Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. – *Ecology* 90: 1301–1313.
- Morris, W. F. and Doak, D. F. 2002. *Quantitative conservation biology: theory and practice of population viability analysis*. – Sinauer Associates Inc.
- Morris, W. F. and Doak, D. F. 2004. Buffering of life histories against environmental stochasticity: accounting for a spurious correlation between the variabilities of vital rates and their contributions to fitness. – *Am. Nat.* 163: 579–590.
- Murray, A. 1866. *The geographical distribution of mammals*. – Day and Son.
- Nenzén, H. K., Swab, R. M., Keith, D. A. and Araújo, M. B. 2012. demoniche – an R-package for simulating spatially-explicit population dynamics. – *Ecography* 35: 577–580.
- NEON (National Ecological Observatory Network) 2025. Small mammal box trapping (DP1.10072.001). – <https://doi.org/10.48443/yrh2-6058>. Dataset accessed from <https://data.onscience.org/data-products/DP1.10072.001/RELEASE-2025> on 1/8/2025
- Nieto-Lugilde, D., Lenoir, J., Abdulkhak, S., Aeschmann, D., Dullinger, S., Gégout, J.-C., Guisan, A., Pauli, H., Renaud, J., Theurillat, J.-P., Thuiller, W., Van Es, J., Vittoz, P., Willner, W., Wohlgenuth, T., Zimmermann, N. E. and Svenning, J.-C. 2015. Tree cover at fine and coarse spatial grains interacts with shade tolerance to shape plant species distributions across the Alps. – *Ecography* 38: 578–589.
- Numata, S., Yasuda, M., Okuda, T., Kachi, N. and Noor, N. S. Md. 2003. Temporal and spatial patterns of mass flowerings on the Malay Peninsula. – *Am. J. Bot.* 90: 1025–1031.
- Numata, S., Yamaguchi, K., Shimizu, M., Sakurai, G., Morimoto, A., Alias, N., Noor Azman, N. Z., Hosaka, T. and Satake, A. 2022. Impacts of climate change on reproductive phenology in tropical rainforests of southeast Asia. – *Commun. Biol.* 5: 311.
- Odling-Smee, F. J., Laland, K. N. and Feldman, M. W. 2003. *Niche construction: the neglected process in evolution*. – Princeton Univ. Press.
- Olson, M. H. 1996. Ontogenetic niche shifts in largemouth bass: variability and consequences for first-year growth. – *Ecology* 77: 179–190.
- Olsoy, P. J., Zaiats, A., Delparte, D. M., Germino, M. J., Richardson, B. A., Roser, A. V., Forbey, J. S., Cattau, M. E. and Caughlin, T. T. 2024. Demography with drones: detecting growth and survival of shrubs with unoccupied aerial systems. – *Restor. Ecol.* 32: e14106.
- Osorio-Olvera, L., Soberón, J. and Falconi, M. 2019. On population abundance and niche structure. – *Ecography* 42: 1415–1425.
- Osorio-Olvera, L., Yáñez-Arenas, C., Martínez-Meyer, E. and Peterson, A. T. 2020. Relationships between population densities and niche-centroid distances in North American birds. – *Ecol. Lett.* 23: 555–564.
- Ovaskainen, O., Roy, D. B., Fox, R. and Anderson, B. J. 2016. Uncovering hidden spatial structure in species communities

- with spatially explicit joint species distribution models. – *Methods Ecol. Evol.* 7: 428–436.
- Ovaskainen, O., Tikhonov, G., Norberg, A., Guillaume Blanchet, F., Duan, L., Dunson, D., Roslin, T. and Abrego, N. 2017. How to make more out of community data? A conceptual framework and its implementation as models and software. – *Ecol. Lett.* 20: 561–576.
- Owen, J. 2023. mpmsim: simulation of matrix population models with defined life history characteristics. – *Methods Ecol. Evol.* 16: 904–911.
- Owens, H. L., Campbell, L. P., Dornak, L. L., Saupe, E. E., Barve, N., Soberón, J., Ingenloff, K., Lira-Noriega, A., Hensz, C. M., Myers, C. E. and Peterson, A. T. 2013. Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. – *Ecol. Modell.* 263: 10–18.
- Pagel, J., Treurnicht, M., Bond, W. J., Kraaij, T., Nottebrock, H., Schutte-Vlok, A., Tonnabel, J., Esler, K. J. and Schurr, F. M. 2020. Mismatches between demographic niches and geographic distributions are strongest in poorly dispersed and highly persistent plant species. – *Proc. Natl Acad. Sci. USA* 117: 3663–3669.
- Pang, S. E. H., Zeng, Y., De Alban, J. D. T. and Webb, E. L. 2022. Occurrence–habitat mismatching and niche truncation when modelling distributions affected by anthropogenic range contractions. – *Divers. Distrib.* 28: 1327–1343.
- Pang, S. E. H., Slik, J. W. F., Chisholm, R. A. and Webb, E. L. 2024. Conserving Southeast Asian trees requires mitigating both climate and land-use change. – *Nat. Sustain.* 7: 1313–1323.
- Pang, S. E. H. et al. 2025. Plant range disequilibrium in Europe is shaped more by disturbance than climate change. – *Research Square*, doi:10.21203/rs.3.rs-6681466/v1.
- Paniw, M., Ozgul, A. and Salguero-Gómez, R. 2018. Interactive life-history traits predict sensitivity of plants and animals to temporal autocorrelation. – *Ecol. Lett.* 21: 275–286.
- Paniw, M., Maag, N., Cozzi, G., Clutton-Brock, T. and Ozgul, A. 2019. Life history responses of meerkats to seasonal changes in extreme environments. – *Science* 363: 631–635.
- Pausas, J. G. and Keeley, J. E. 2014. Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. – *New Phytol.* 204: 55–65.
- Pearman, P. B., Guisan, A., Broennimann, O. and Randin, C. F. 2008. Niche dynamics in space and time. – *Trends Ecol. Evol.* 23: 149–158.
- Pearse, I. S., LaMontagne, J. M., Lordon, M., Hipp, A. L. and Koenig, W. D. 2020. Biogeography and phylogeny of masting: do global patterns fit functional hypotheses? – *New Phytol.* 227: 1557–1567.
- Pearse, I. S., Wion, A. P., Gonzalez, A. D. and Pendorfer, M. B. 2021. Understanding mast seeding for conservation and land management. – *Philos. Trans. R. Soc. B* 376: 20200383.
- Peng, S., Ramirez-Parada, T. H., Mazer, S. J., Record, S., Park, I., Ellison, A. M. and Davis, C. C. 2024. Incorporating plant phenological responses into species distribution models reduces estimates of future species loss and turnover. – *New Phytol.* 242: 2338–2352.
- Pennekamp, F., Monteiro, E. and Schmitt, T. 2013. The larval ecology of the butterfly *Euphydryas desfontainii* (Lepidoptera: Nymphalidae) in SW-Portugal: food plant quantity and quality as main predictors of habitat quality. – *J. Insect Conserv.* 17: 195–206.
- Perez-Navarro, M. A., Broennimann, O., Esteve, M. A., Bagaria, G., Guisan, A. and Lloret, F. 2022. Comparing climatic suitability and niche distances to explain populations responses to extreme climatic events. – *Ecography* 2022: e06263.
- Persson, D., Halberg, K. A., Jørgensen, A., Ricci, C., Møbjerg, N. and Kristensen, R. M. 2011. Extreme stress tolerance in tardigrades: surviving space conditions in low earth orbit. – *J. Zool. Syst. Evol. Res.* 49: 90–97.
- Peterson, A. T., Soberón, J., Pearson, R. G., Anderson, R. P., Martínez-Meyer, E., Nakamura, M. and Araujo, M. B. 2011. Ecological niches and geographic distributions. – Princeton Univ. Press.
- Peterson, A. T., Cobos, M. E. and Jiménez-García, D. 2018. Major challenges for correlational ecological niche model projections to future climate conditions: climate change, ecological niche models, and uncertainty. – *Ann. N. Y. Acad. Sci.* 1429: 66–77.
- Peterson, A. T., Soberón, J., Ramsey, J. and Osorio-Olvera, L. 2020. Co-occurrence networks do not support identification of biotic interactions. – *Biodiv. Inform.* 15: 1–10.
- Pethybridge, H., Roos, D., Loizeau, V., Pecquerie, L. and Bacher, C. 2013. Responses of European anchovy vital rates and population growth to environmental fluctuations: an individual-based modeling approach. – *Ecol. Modell.* 250: 370–383.
- Pfister, C. A. 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. – *Proc. Natl Acad. Sci. USA* 95: 213–218.
- Pilowsky, J. A., Colwell, R. K., Rahbek, C. and Fordham, D. A. 2022. Process-explicit models reveal the structure and dynamics of biodiversity patterns. – *Sci. Adv.* 8: eabj2271.
- Pironon, S., Vilellas, J., Morris, W. F., Doak, D. F. and García, M. B. 2015. Do geographic, climatic or historical ranges differentiate the performance of central versus peripheral populations? – *Global Ecol. Biogeogr.* 24: 611–620.
- Pironon, S., Papuga, G., Vilellas, J., Angert, A. L., García, M. B. and Thompson, J. D. 2017. Geographic variation in genetic and demographic performance: new insights from an old biogeographical paradigm. – *Biol. Rev.* 92: 1877–1909.
- Pironon, S., Vilellas, J., Thuiller, W., Eckhart, V. M., Geber, M. A., Moeller, D. A. and García, M. B. 2018. The ‘Hutchinsonian niche’ as an assemblage of demographic niches: implications for species geographic ranges. – *Ecography* 41: 1103–1113.
- Pistón, N., Bello, F., Dias, A. T. C., Götzenberger, L., Rosado, B. H. P., Mattos, E. A., Salguero-Gómez, R. and Carmona, C. P. 2019. Multidimensional ecological analyses demonstrate how interactions between functional traits shape fitness and life history strategies. – *J. Ecol.* 107: 2317–2328.
- Poggiato, G., Münkemüller, T., Bystrova, D., Arbel, J., Clark, J. S. and Thuiller, W. 2021. On the interpretations of joint modeling in community ecology. – *Trends Ecol. Evol.* 36: 391–401.
- Pollock, L. J., Morris, W. K. and Vesk, P. A. 2012. The role of functional traits in species distributions revealed through a hierarchical model. – *Ecography* 35: 716–725.
- Pollock, L. J., Tingley, R., Morris, W. K., Golding, N., O’Hara, R. B., Parris, K. M., Vesk, P. A. and McCarthy, M. A. 2014. Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). – *Methods Ecol. Evol.* 5: 397–406.
- Ponti, R. and Sannolo, M. 2023. The importance of including phenology when modelling species ecological niche. – *Ecography* 2023: e06143.
- Poole, A. E., Stillman, R. A., Watson, H. K. and Norris, K. J. 2007. Searching efficiency and the functional response of a pause-travel forager. – *Funct. Ecol.* 21: 784–792.

- Poorter, L. 2007. Are species adapted to their regeneration niche, adult niche, or both? – *Am. Nat.* 169: 433–442.
- Post, E. 2019. The phenological niche. Time in ecology. A theoretical framework [MPB 61]. – Princeton Univ. Press, pp. 67–93.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. – *Am. Nat.* 132: 652–661.
- Pulliam, H. R. 2000. On the relationship between niche and distribution. – *Ecol. Lett.* 3: 349–361.
- Pulliam, H. R. and Danielson, B. J. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. – *Am. Nat.* 137: S50–S66.
- Qiao, H., Saupe, E. E., Soberón, J., Peterson, A. T. and Myers, C. E. 2016. Impacts of niche breadth and dispersal ability on macroevolutionary patterns. – *Am. Nat.* 188: 149–162.
- Rangel, T. F. L. V. B., Diniz-Filho, J. A. F. and Colwell, R. K. 2007. Species richness and evolutionary niche dynamics: a spatial pattern-oriented simulation experiment. – *Am. Nat.* 170: 602–616.
- Reed, T. E., Waples, R. S., Schindler, D. E., Hard, J. J. and Kinison, M. T. 2010. Phenotypic plasticity and population viability: the importance of environmental predictability. – *Proc. R. Soc. B* 277: 3391–3400.
- Rees, M. and Ellner, S. P. 2009. Integral projection models for populations in temporally varying environments. – *Ecol. Monogr.* 79: 575–594.
- Requena-Mullor, J. M., Maguire, K. C., Shinneman, D. J. and Caughlin, T. T. 2019. Integrating anthropogenic factors into regional-scale species distribution models – a novel application in the imperiled sagebrush biome. – *Global Change Biol.* 25: 3844–3858.
- Rosen, A., Battison, R., Hernández, C. M., Spacey, O., McLean, J., Prober, S., Gascoigne, S., McMahon, S., Jucker, T. and Salguero-Gómez, R. 2025. Modelling forest dynamics using integral projection models (IPMs) and repeat LiDAR. – bioRxiv, doi:10.1101/2025.01.06.631514.
- Rumpf, S. B., Hülber, K., Wessely, J., Willner, W., Moser, D., Gatringer, A., Klöner, G., Zimmermann, N. E. and Dullinger, S. 2019. Extinction debts and colonization credits of non-forest plants in the European Alps. – *Nat. Commun.* 10: 4293.
- Rutrough, A., Widick, I. V. and Bean, W. T. 2019. Reconstruction of the historical range alters niche estimates in an endangered rodent. – *Ecography* 42: 1742–1751.
- Sagarin, R. D. and Gaines, S. D. 2002. The ‘abundant centre’ distribution: to what extent is it a biogeographical rule? – *Ecol. Lett.* 5: 137–147.
- Salguero-Gómez, R. 2018. Implications of clonality for ageing research. – *Evol. Ecol.* 32: 9–28.
- Salguero-Gómez, R. and De Kroon, H. 2010. Matrix projection models meet variation in the real world. – *J. Ecol.* 98: 250–254.
- Salguero-Gómez, R. et al. 2015. The compadre plant matrix database: an open online repository for plant demography. – *J. Ecol.* 103: 202–218.
- Salguero-Gómez, R. et al. 2016a. COMADRE: a global data base of animal demography. – *J. Anim. Ecol.* 85: 371–384.
- Salguero-Gómez, R., Jones, O. R., Jongejans, E., Blomberg, S. P., Hodgson, D. J., Mbeau-Ache, C., Zuidema, P. A., de Kroon, H. and Buckley, Y. M. 2016b. Fast–slow continuum and reproductive strategies structure plant life-history variation worldwide. – *Proc. Natl Acad. Sci. USA* 113: 230–235.
- Salguero-Gómez, R., Violle, C., Gimenez, O. and Childs, D. 2018. Delivering the promises of trait-based approaches to the needs of demographic approaches, and vice versa. – *Funct. Ecol.* 32: 1424–1435.
- Santini, L., Pironon, S., Maiorano, L. and Thuiller, W. 2019. Addressing common pitfalls does not provide more support to geographical and ecological abundant-centre hypotheses. – *Ecography* 42: 696–705.
- Santos, G. S., Salguero-Gómez, R., Dias, A. T. C. and Kajin, M. 2021. To buffer or to be labile? A framework to disentangle demographic patterns and evolutionary processes. – bioRxiv, doi:10.1101/2021.04.12.439165.
- Saupe, E. E., Barve, V., Myers, C. E., Soberón, J., Barve, N., Hensz, C. M., Peterson, A. T., Owens, H. L. and Lira-Noriega, A. 2012. Variation in niche and distribution model performance: the need for a priori assessment of key causal factors. – *Ecol.* 237–238: 11–22.
- Sax, D. F., Early, R. and Bellemare, J. 2013. Niche syndromes, species extinction risks, and management under climate change. – *Trends Ecol. Evol.* 28: 517–523.
- Schimper, A. F. W. 1902. Plant-geography upon a physiological basis. – Clarendon Press.
- Schurr, F. M., Pagel, J., Cabral, J. S., Groeneveld, J., Bykova, O., O’Hara, R. B., Hartig, F., Kissling, W. D., Linder, H. P., Midgley, G. F., Schröder, B., Singer, A. and Zimmermann, N. E. 2012. How to understand species’ niches and range dynamics: a demographic research agenda for biogeography: a demographic research agenda for biogeography. – *J. Biogeogr.* 39: 2146–2162.
- Sexton, J. P., McIntyre, P. J., Angert, A. L. and Rice, K. J. 2009. Evolution and ecology of species range limits. – *Annu. Rev. Ecol. Evol. Syst.* 40: 415–436.
- Sheth, S. N. and Angert, A. L. 2018. Demographic compensation does not rescue populations at a trailing range edge. – *Proc. Natl Acad. Sci. USA* 115: 2413–2418.
- Simon, M. W. and Amarasekare, P. 2024. Predicting the fundamental thermal niche of ectotherms. – *Ecology* 105: e4289.
- Smith, T. G. and Stirling, I. 1975. The breeding habitat of the ringed seal (*Phoca hispida*). The birth lair and associated structures. – *Can. J. Zool.* 53: 1297–1305.
- Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. – *Ecol. Lett.* 10: 1115–1123.
- Soberón, J. and Peterson, A. T. 2005. Interpretation of models of fundamental ecological niches and species’ distributional areas. – *Biodiv. Inform.* 2: 1–10.
- Soberón, J. and Nakamura, M. 2009. Niches and distributional areas: concepts, methods, and assumptions. – *Proc. Natl Acad. Sci. USA* 106: 19644–19650.
- Soberón, J. and Peterson, A. T. 2020. What is the shape of the fundamental Grinnellian niche? – *Theor. Ecol.* 13: 105–115.
- Sprengel, C. 1827. Ueber Pflanzenhumus, Humussäure und humussäure Salze (About plant humus, humic acids and salts of humic acids). – *Arch. Pharmazie* 21: 261–263.
- Stearns, S. C. 1992. The evolution of life histories. – Oxford Univ. Press.
- Stearns, S. C. and Koella, J. C. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. – *Evolution* 40: 893–913.
- Stephens, P. A., Sutherland, W. J. and Freckleton, R. P. 1999. What is the allee effect? – *Oikos* 87: 185–190.
- Sutherland, W. J. et al. 2013. Identification of 100 fundamental ecological questions. – *J. Ecol.* 101: 58–67.
- Svenning, J. and Skov, F. 2004. Limited filling of the potential range in European tree species. – *Ecol. Lett.* 7: 565–573.
- Svenning, J. and Sandel, B. 2013. Disequilibrium vegetation dynamics under future climate change. – *Am. J. Bot.* 100: 1266–1286.

- Svenning, J.-C., Buitenwerf, R. and Le Roux, E. 2024. Trophic rewilding as a restoration approach under emerging novel biosphere conditions. – *Curr. Biol.* 34: R435–R451.
- Swanson, H. K., Lysy, M., Power, M., Stasko, A. D., Johnson, J. D. and Reist, J. D. 2015. A new probabilistic method for quantifying n-dimensional ecological niches and niche overlap. – *Ecology* 96: 318–324.
- Tavecchia, G., Coulson, T., Morgan, B. J. T., Pemberton, J. M., Pilkington, J. C., Gulland, F. M. D. and Clutton-Brock, T. H. 2005. Predictors of reproductive cost in female Soay sheep. – *J. Anim. Ecol.* 74: 201–213.
- Teller, B. J., Adler, P. B., Edwards, C. B., Hooker, G. and Ellner, S. P. 2016. Linking demography with drivers: climate and competition. – *Methods Ecol. Evol.* 7: 171–183.
- Ten Caten, C. and Dallas, T. 2025. Population variability across geographical ranges: perspectives and challenges. – *Proc. R. Soc. B* 292: 20241644.
- Thuiller, W., Richardson, D. M., Pyšek, P., Midgley, G. F., Hughes, G. O. and Rouget, M. 2005. Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. – *Global Change Biol.* 11: 2234–2250.
- Tourinho, L. and Vale, M. M. 2023. Choosing among correlative, mechanistic, and hybrid models of species' niche and distribution. – *Integr. Zool.* 18: 93–109.
- Treurnicht, M., Pagel, J., Tonnabel, J., Esler, K. J., Slingsby, J. A. and Schurr, F. M. 2020. Functional traits explain the Hutchinsonian niches of plant species. – *Global Ecol. Biogeogr.* 29: 534–545.
- Tuljapurkar, S. D. and Orzack, S. H. 1980. Population dynamics in variable environments I. Long-run growth rates and extinction. – *Theor. Popul. Biol.* 18: 314–342.
- Tuljapurkar, S., Horvitz, C. C. and Pascarella, J. B. 2003. The many growth rates and elasticities of populations in random environments. – *Am. Nat.* 162: 489–502.
- Tuljapurkar, S., Gaillard, J.-M. and Coulson, T. 2009. From stochastic environments to life histories and back. – *Phil. Trans. R. Soc. B* 364: 1499–1509.
- Vacchiano, G., Hackett-Pain, A., Turco, M., Motta, R., Maringer, J., Conedera, M., Drobyshchev, I. and Ascoli, D. 2017. Spatial patterns and broad-scale weather cues of beech mast seeding in Europe. – *New Phytol.* 215: 595–608.
- van Noordwijk, A. J. and de Jong, G. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. – *Am. Nat.* 128: 137–142.
- Vandermeer, J. H. 1972. Niche theory. – *Annu. Rev. Ecol. Syst.* 1972: 107–132.
- Villellas, J., Doak, D. F., García, M. B. and Morris, W. F. 2015. Demographic compensation among populations: what is it, how does it arise and what are its implications? – *Ecol. Lett.* 18: 1139–1152.
- Villellas, J. et al. 2021. Phenotypic plasticity masks range-wide genetic differentiation for vegetative but not reproductive traits in a short-lived plant. – *Ecol. Lett.* 24: 2378–2393.
- Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. and Garnier, E. 2007. Let the concept of trait be functional! – *Oikos* 116: 882–892.
- Von Euler, T., Ågren, J. and Ehrlén, J. 2014. Environmental context influences both the intensity of seed predation and plant demographic sensitivity to attack. – *Ecology* 95: 495–504.
- Wardle, G. M. and Buckley, Y. M. 2014. PlantPopNet: a spatially distributed model system for population ecology (ecology society of Australia 2014 annual conference). – Alice Springs NT (in press).
- Warton, D. I., Shipley, B. and Hastie, T. 2015a. CATS regression – a model-based approach to studying trait-based community assembly. – *Methods Ecol. Evol.* 6: 389–398.
- Warton, D. I., Blanchet, F. G., O'Hara, R. B., Ovaskainen, O., Taskinen, S., Walker, S. C. and Hui, F. K. C. 2015b. So many variables: joint modeling in community ecology. – *Trends Ecol. Evol.* 30: 766–779.
- Weber, M. M., Stevens, R. D., Diniz-Filho, J. A. F. and Grelle, C. E. V. 2017. Is there a correlation between abundance and environmental suitability derived from ecological niche modelling? A meta-analysis. – *Ecography* 40: 817–828.
- Werner, E. E. and Gilliam, J. F. 1984. The ontogenetic niche and species interactions in size-structured populations. – *Annu. Rev. Ecol. Syst.* 15: 393–425.
- Wiegand, T., Moloney, K. A., Naves, J. and Knauer, F. 1999. Finding the missing link between landscape structure and population dynamics: a spatially explicit perspective. – *Am. Nat.* 154: 605–627.
- Willner, W., Wessely, J., Gattringer, A., Moser, D., Závieská, E., Dullinger, S., Schönswetter, P. and Hülber, K. 2023. Post-glacial range formation of temperate forest understorey herbs – insights from a spatio-temporally explicit modelling approach. – *Global Ecol. Biogeogr.* 32: 1046–1058.
- Wisz, M. S. et al. 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. – *Biol. Rev.* 88: 15–30.
- Wright, S. J., Muller-Landau, H. C., Condit, R. and Hubbell, S. P. 2003. Gap-dependent recruitment, realised vital rates, and size distributions of tropical trees. – *Ecology* 84: 3174–3185.
- Yañez-Arenas, C., Martínez-Meyer, E., Mandujano, S. and Rojas-Soto, O. 2012. Modelling geographic patterns of population density of the white-tailed deer in central Mexico by implementing ecological niche theory. – *Oikos* 121: 2081–2089.
- Young, T. P., Petersen, D. A. and Clary, J. J. 2005. The ecology of restoration: historical links, emerging issues and unexplored realms. – *Ecol. Lett.* 8: 662–673.
- Zanatta, F., Engler, R., Collart, F., Broennimann, O., Mateo, R. G., Papp, B., Muñoz, J., Baurain, D., Guisan, A. and Vanderpoorten, A. 2020. Bryophytes are predicted to lag behind future climate change despite their high dispersal capacities. – *Nat. Commun.* 11: 5601.
- Zanden, H. B. V., Arthur, K. E., Bolten, A. B., Popp, B. N., Lagueux, C. J., Harrison, E., Campbell, C. L. and Bjorndal, K. A. 2013. Trophic ecology of a green turtle breeding population. – *Mar. Ecol. Prog. Ser.* 476: 237–249.
- Zurell, D. 2017. Integrating demography, dispersal and interspecific interactions into bird distribution models. – *J. Avian Biol.* 48: 1505–1516.
- Zurell, D., Jeltsch, F., Dormann, C. F. and Schröder, B. 2009. Static species distribution models in dynamically changing systems: how good can predictions really be? – *Ecography* 32: 733–744.
- Zurell, D., Zimmermann, N. E. and Brun, P. 2024. The niche through time: considering phenology and demographic stages in plant distribution models. – *J. Ecol.* 112: 1926–1939.