

REVIEW

Grime Review: How Do Species Distribution Models Reflect and Inform Ecological Processes?

The niche through time: Considering phenology and demographic stages in plant distribution models

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Handling Editor: Charlotte Ndiribe**Abstract**

- Species distribution models (SDMs) are widely used to infer species–environment relationships, predict spatial distributions and characterise species' environmental niches. While the importance of space and spatial scales is widely acknowledged in SDM applications, temporal components of the niche are rarely addressed.
- We discuss how phenology and demographic stages affect model inference in plant SDMs. Ignoring conspicuousness and timing of phenological stages may bias niche estimates through increased observer bias, while ignoring stand age may bias niche estimates through temporal mismatches with environmental variables, especially during times of rapid global warming.
- We present different methods to consider phenology and demographic stages in plant SDMs, including the selection of causal, spatiotemporally explicit predictors and the calibration of stage-specific SDMs. Based on a case study with citizen science data, we illustrate how spatiotemporal SDMs provide deeper insights on the coincidence of range and phenological shifts under climate change.
- The proliferation of digitally available biodiversity and citizen science data increasingly allows considering time explicitly in SDMs. This offers a more mechanistic understanding of plant distributions, and more robust predictions under global change, especially if the reporting of phenological stages and age is facilitated and promoted by relevant data portals.

KEY WORDS

citizen science, climate change, demography, ecological niche models, life stages, phenology, species distribution models

1 | INTRODUCTION

Why do species occur at specific locations but not elsewhere? This is a central question in ecology and biogeography and has become ever more relevant as climate change is causing major species redistributions across the globe (Lenoir et al., 2020; Pecl et al., 2017).

With the increasing availability of georeferenced species observations and gridded environmental data (Wüest et al., 2020), correlative species distribution models (SDMs) have become a powerful tool for understanding and predicting species distributions (Elith & Leathwick, 2009; Guisan et al., 2017; Guisan & Zimmermann, 2000). SDMs relate observed species occurrences to prevailing

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environmental conditions, using appropriate statistical and machine learning techniques. The fitted species–environment relationship can then be interpreted as the hypothesised species environmental preferences or can be used to predict the occurrence probability of a species for a given set of environmental conditions. Potential applications of SDMs are manifold, ranging from testing hypotheses about species' ecology and range determinants (Chauvier, Thuiller, et al., 2021; Normand et al., 2009; Zimmermann et al., 2009), biogeographic history (Normand et al., 2011), to informing protected area design (Albert et al., 2017; Chauvier et al., 2024), and predicting potential future distributions and threat status under scenarios of climate change (Brun et al., 2020; Zurell et al., 2018, 2023).

SDMs are tightly linked to the niche concept. The ecological niche comprises all environmental conditions that allow positive population growth and under which the species can persist indefinitely (usually characterised by successful reproduction and survival) (Hutchinson, 1957). As the interest in SDM applications grew immensely over the last three decades, much attention has been given to method development (Brun et al., 2020; Chauvier, Zimmermann, et al., 2021), method testing (Elith et al., 2006; Valavi et al., 2022) and definition and implementation of standards (Araújo et al., 2019; Zurell et al., 2020). Also, the role of spatial scale and scale dependency has been widely acknowledged (Guisan & Thuiller, 2005) and tested (Adde et al., 2023; König et al., 2021). It is generally accepted that (macro-)climate drives large-scale species distributions while factors related to habitat availability and soil resources but also topography and microclimate drive small-scale variations in species occurrence (Descombes et al., 2020; Guisan & Thuiller, 2005; Lembrechts et al., 2019; McGill, 2010). Thus, the components of the niche that can be identified by SDMs depend on the spatial resolution and extent of the data and analyses. By contrast, the role of time has been less often discussed in the context of SDMs (Ponti & Sannolo, 2023). Here, we argue that temporal components related to species' phenological and demographic stages can be highly relevant for fitting plant SDMs. Phenological events like budburst, flowering and seed set are related to specific environmental conditions that will determine successful reproduction and survival at any given location. Changes in plant phenology have been reported in response to climate change with potential effects cascading through entire food webs and ecosystems (Scheffers et al., 2016; Vitasse et al., 2022). Additionally, phenology may mediate the detection probability of species across space as some phenological stages might be more conspicuous than others. Demographic stages (or life stages) describe key phases in the life cycle of a species that may differ substantially in their environmental tolerance, for example in response to environmental conditions, such as frost, and limited availability of resources, such as water. For example, the juveniles of many tree species have been found to have narrower climatic niches than adults (Dobrowski et al., 2015; Ellenberg, 2009). Ignoring the relevance of phenological and demographic stages for detecting the species and for identifying range-limiting factors could lead to biased niche estimates in SDMs and to fallacious predictions into the future.

In this review, we aim to draw attention to temporal components of the niche and how they are typically considered (or not) in SDMs. We illuminate this topic with a systematic literature review and discuss conceptual and methodological perspectives. First, we identify relevant temporal components of species–environment relationships and conduct a Web of Science literature search to assess the current representation of temporal components in plant SDMs. Second, we discuss these temporal components in more detail and reflect on the niche concept in light of environmental seasonality and species' ontogeny and potential consequences for SDM calibration and inference. Last, we provide an overview of methods that can be used for considering phenology and demographic stages in SDMs and discuss opportunities and challenges for future research. Our review emphasises that explicitly considering temporal components of the niche in SDMs allows an improved mechanistic understanding of niche and range determinants and deeper insights into species spatial and temporal response to historic as well as contemporary climate change.

2 | TEMPORAL COMPONENTS OF THE NICHE

Species distribution models relate occurrence records to environmental predictor variables to establish a species–environment relationship that is indicative of a species' environmental niche. Conceptually, we can distinguish between the fundamental niche, which is described by all environmental conditions that allow indefinite survival of a species in the absence of interspecific competition, meaning non-negative population growth and the realised niche, which additionally considers population survival in the presence of interacting species (Colwell & Rangel, 2009). For the purpose of this review, however, this distinction is not overly important, and we simply use the term 'niche'. Here, we are mainly interested in temporal components of the niche. Typically, the environmental conditions to which plants are exposed show substantial seasonal and interannual variations. Their phenological stages and life cycles are often synchronised with the seasons and can experience very different environmental conditions (Figure 1). Annual cycles and phenology may be affected by seasonality in climate, daylight hours and radiation at higher latitudes, or by seasonality in precipitation at lower latitudes. Similarly, the life cycles of long-lived species stretch over decades to centuries, and their demographic stages may experience considerable variations in environmental conditions, resulting from stochastic differences in environmental conditions and from systematic climate change. Climate, by definition, describes long-term weather patterns, typically averaged over a reference period of 25–30 years (Arguez & Vose, 2011; Karger et al., 2017). Relating species occurrences to such (species-unspecific) reference periods describing the average climatic conditions of the past 30 years may preclude understanding of the effects of shorter- and longer-term variability and with that prevent a more mechanistic understanding of relevant niche and range determinants.

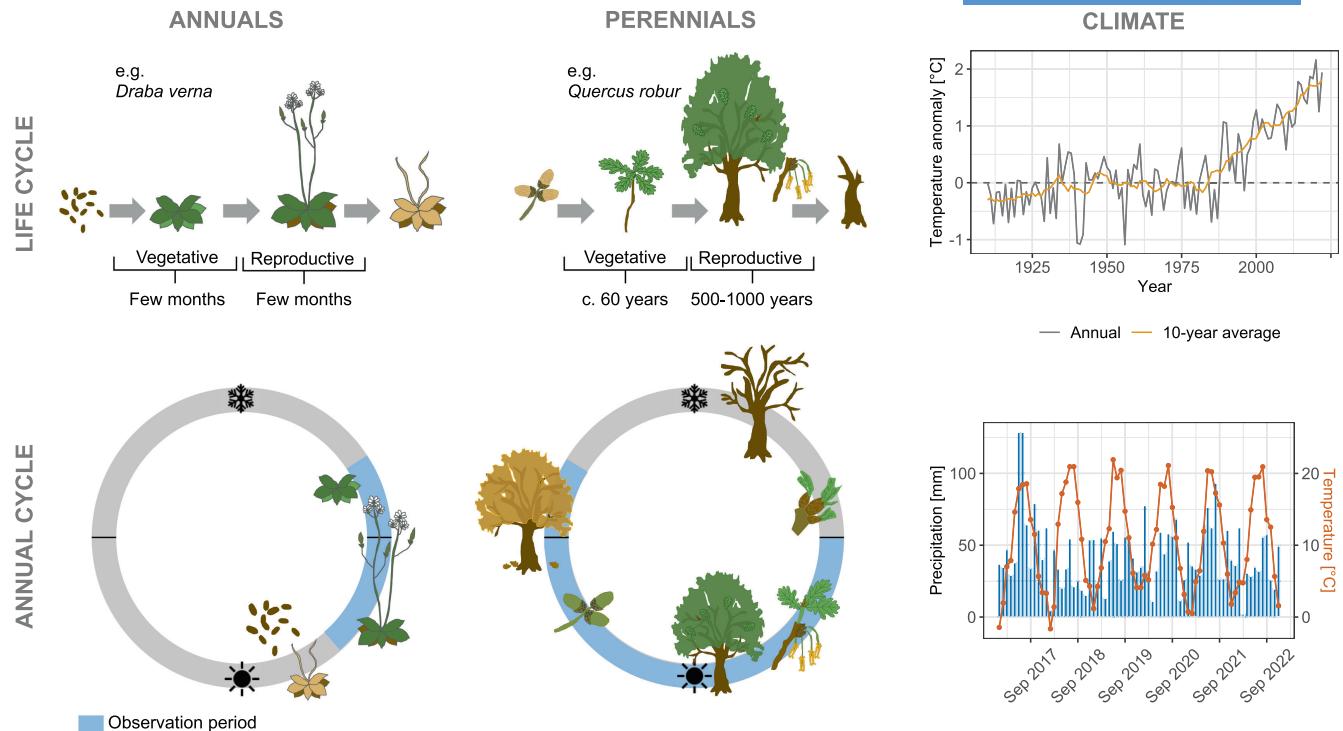


FIGURE 1 Exemplary life cycles, annual cycles and corresponding observation periods of annual (left) and perennial plants (centre) in temperate regions. The annual common whitlowgrass (*Draba verna*) is a very short-lived therophyte that undergoes the vegetative and reproductive growth phases within a few months and survives the cold winters as seeds. It can only be observed early in the year. The pedunculate oak (*Quercus robur*) is a very long-lived, temperate tree species that takes decades to reach maturity and enter the reproductive phase. It is easily confused with the sessile oak (*Quercus petraea*); the two can be distinguished by the auricles of their leaves and the peduncles of the acorns, that is, ideally within the vegetation period. The right panels show the annual temperature anomalies in Europe over the past 100 years (from NOAA National Centers for Environmental information) and the monthly precipitation and temperature in Berlin, Germany, over the past 6 years (from Deutscher Wetterdienst DWD). For perennials like the oak, the climatic conditions experienced during establishment can strongly differ from the current climatic conditions due to interannual fluctuations and climatic trends. The exact timing of phenological stages throughout the annual cycle can vary between years and across space due to variations in weather between years. Panels with life and annual cycles inspired by (Wang & Ding, 2023).

2.1 | Literature search

We conducted a keyword-based search in the Web of Science to quantify how often temporal components related to phenology and demographic stages are explicitly considered in plant SDMs. A full list of keywords is provided in Table S1. We used a nested set of keywords to identify all studies that mentioned SDMs (or common synonyms), were focused on plants and were listing relevant keywords related to phenology or to demographic stages, respectively. The search was carried out on 5 October 2023 and was restricted to English-language journal articles in the period 1945–2022 (no studies using SDMs were published before that start year). Overall, we found more than 40,000 articles mentioning SDM and over 10,000 articles in our refined search for plant SDMs, with a strong increase in the number of articles over time (Figure 2). Among these, phenology (or related search terms) was mentioned in 970 articles and demographic stages (or related terms) in 1188 articles, each averaging c. 10% of the plant SDM articles. The search categories phenology and demographic stages, thereby, were largely mutually exclusive.

For each search category, phenology and demographic stages, we assessed a random subset of 300 articles to gain more insights

about how these temporal components of the niche were considered in SDMs. To do so, we separated all articles published after 1990 in 11-year bins (1990–2000, 2001–2011 and 2012–2022) and aimed at assessing 100 papers per bin and category (phenology vs. demographic stages). As fewer than 100 papers were published in the first time period (1990–2000), we drew slightly more articles from the latter two periods. This resulted in sample sizes of $n=28$, $n=123$ and $n=149$ of publications mentioning phenology in the three 11-year bins, respectively, and $n=41$, $n=130$ and $n=129$ mentioning demographic stages. We then scanned the abstracts for information that the articles indeed fitted plant SDMs and explicitly considered phenology or demographic stages (Table S2). In cases where the abstract was inconclusive, we also scanned the methods. If the papers fulfilled these search criteria, we extracted additional information from abstract and methods regarding the taxa and region studied, and spatial and temporal scale (cf. Supporting Data Table, Zurell et al., 2024). Importantly, we found that only 32% of the identified articles indeed fitted plant SDMs, and only 2% and 4% explicitly considered phenology and demographic stages, respectively. Thus, the keyword-based literature search largely overestimated the number of studies employing SDMs, and especially the number of studies

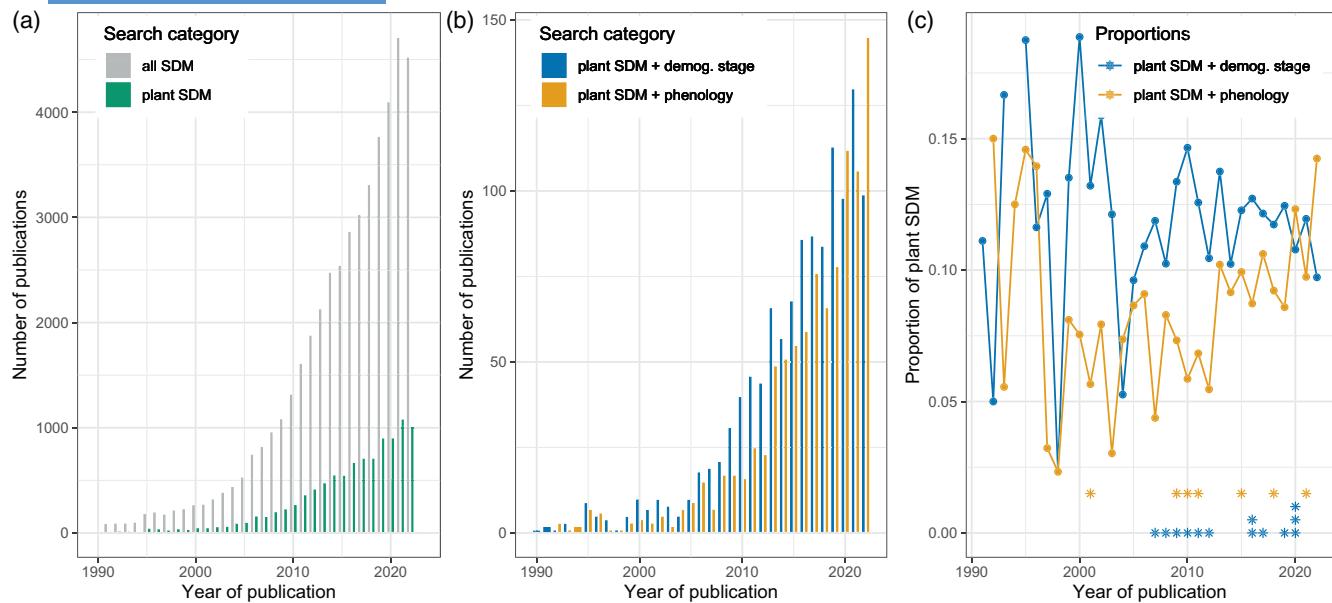


FIGURE 2 Web of Science search results (see Table S1 for keywords used in the search). We restrict the display to publications that appeared after 1990 as only two studies on plant species distribution model (SDM) were published earlier. (a) shows the total number of SDM publications and those exclusively focusing on plants. (b) shows the absolute number of plant SDM publications that mentioned demographic stages or phenology. (c) shows the proportional number of plant SDM publications that mentioned demographic stages or phenology. Asterisks indicate the year and number of publications that explicitly considered phenology and demographic stages in plant SDMs as identified in our detailed review of random subsets of 300 papers per search category (phenology and demographic stages).

that explicitly dealt with temporal niche components. Demographic stages were thereby considered slightly more often than phenology (Figure 2), and most of these studies occurred from 2010 onwards and focussed on tree species (Supporting Data Table, Zurell et al., 2024). Given these small sample sizes, we did not conduct any further statistical analyses based on the relevant papers identified. Yet, in the following, we provide more in-depth conceptual considerations how phenology and demographic stages affect SDM estimates (Table 1), a synthesis of how these aspects have been considered in the literature and the insights gained from these.

2.2 | Demographic or life stages

The ecological niche of a plant determines how it responds to the environment, and this behaviour may depend on age or stage, meaning that juvenile plants may exhibit a different ecological niche than adult ones (e.g. Ellenberg, 2009), or more generally that the niche of a species may vary with its size (Peters, 1983; Werner & Gilliam, 1984). In this review, we refer to demographic stages as age cohorts (juvenile, adult and senescent plants) that often show distinctly different ecological behaviours, and thus allow simplifications in modelling the dynamics of populations (e.g. Bugmann, 2001; Chu & Adler, 2015), in particular of long-lived plants. Explicitly considering demographic stages allows us to assess ecological niche differences that are relevant for and drive demographic processes such as regeneration, persistence and mortality under fluctuating or changing environmental conditions.

For SDMs, demographic stages are specifically relevant when juvenile plants exhibit ecological tolerances that differ from those of adults. From a demographic perspective, a population is only stable over longer time periods, if both regeneration and adult persistence are guaranteed (Figure 3). Most plant species are perennials, and most observations refer to the adult stage where species are easier to distinguish or are more routinely included in inventories. For example, in forest inventories trees are typically only recorded if exceeding a minimum diameter at breast height. Juveniles are usually much smaller and experience different environmental conditions than adults, which often contribute to or form the overall vegetation structure. By that, juveniles are exposed to a different environment, but often they also exhibit different, mostly narrower tolerances to ecological niche factors such as cold or shade tolerance (Figure 3). Jackson et al. (2009) referred to this as differences in the naïve, unitary niche (including adult persistence) and the regeneration niche (allowing successful reproduction and thus being indicative of successful seed establishment and juvenile survival).

In their assessment of six coniferous tree species, Bell et al. (2014) identified significant differences in juvenile compared with adult habitat suitability, specifically at range margins. They demonstrated that the juvenile niche is often less tolerant against extreme climatic conditions than the adult niche. If juveniles exhibit distinct and more narrow niches and tolerances than adult ones, then SDMs trained with adult observations projecting the effect of climate change on species' spatial distribution predict persistence of adults rather than the success of regeneration. Yet, since juvenile

TABLE 1 Potential biases and consequences from non-consideration of temporal niche components in species distribution models.

Potential bias	Consequences
Demographic stages	
Environmental niche differs among demographic stages	Confusion of adult persistence niche and regeneration niche
Adult persistence niche larger than regeneration niche	Overestimation of environmental tolerance, overestimation of habitat suitability for establishment of new populations (e.g. under climate change)
Temporal mismatch between stage age and environmental predictors	Biased niche estimates, underestimation or overestimation of environmental tolerance at niche limits, misinterpretation of limiting niche factors, fallacious predictions of habitat suitability
Phenology	
Environmental tolerance differs among phenological stages	Misidentification of causal predictors and range-limiting factors (e.g. cold and warm range limits might be determined by environmental tolerance of different phenological stages)
Environmental extremes affect specific phenological stages	Misidentification of causal predictors and niche limiting factors (e.g. effect of late frost events on regeneration depends on timing of budburst)
Detectability bias	Non-identification of species (false absences) through early or late phenology (relative to main vegetation period), misidentification (species confusion) through variation of morphological similarity across phenological stages

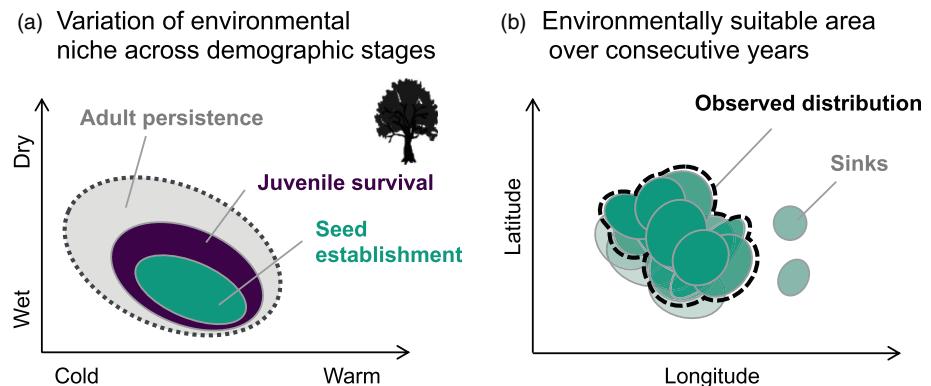


FIGURE 3 Variation of environmental niche across demographic stages and observed distribution of a hypothetical long-lived tree species. (a) Different demographic stages may show different niche requirements. For example, adult trees might be more tolerant towards drought and frost than juveniles. The grey ellipse exemplifies the naïve, unitary niche when fitting SDMs to all available occurrence data, while the intersection of the green and purple ellipse represents the regeneration niche for successful reproduction (Jackson et al., 2009). (b) As environmental conditions vary across years, the environmentally suitable area will vary in space (one circle represents the spatial distribution of juveniles per year, with darker shades indicating younger stands). The species can only be observed in areas where the environment is suitable for adult persistence and where the conditions allowed seed establishment and juvenile survival at any point in time matching the stand's age. Sufficiently frequent seed establishment is needed to ensure long-term population persistence, otherwise seed establishment may lead to sink populations with a single adult age-cohort and without new recruitment.

regeneration is essential to project viable populations under changing environmental conditions, differentiating demographic stages in SDMs, or building separate models for different stages, is essential to add realism to SDM-based projections under changing environmental conditions (Jackson et al., 2009). Since seedling establishment and juvenile survival happen during relatively short demographic stages, it becomes important to temporally match environmental (e.g. climate) data to the relevant observation period of the stage-specific distribution data. Figure 3 illustrates how different demographic stages might differ in environmental space (Figure 3a) and how observations made over longer time periods with annually fluctuating environments might affect the general

distribution of a species (Figure 3b). Such annual fluctuations might primarily affect the juvenile stage such that regeneration might not be possible every year across the whole geographic range. However, if regeneration is possible sufficiently frequently, then populations can be maintained over long time periods despite occasionally unsuitable conditions for juveniles. If, however, regeneration can occur only very rarely, then viable populations cannot establish, and we might expect so-called sink populations with very few or only one age-cohort that simply grows older without further regeneration, until it perishes away (Figure 3) (Pulliam, 2000). Especially for long-lived species under climate change, ignoring demographic stages in SDMs could lead to biased niche estimates

(Table 1). For example, old trees may have established under very different climatic conditions than are observable today (Figure 1) and conventional SDMs may thus overestimate their environmental tolerances. As Jackson et al. (2009) discussed, stage-specific niches, environmental variation and climate change may leave an imprint of historical contingencies in current-day species distributions. Thus, considering temporal components of the niche is not only relevant for anticipating species response to future climate change but also for understanding biogeographic history.

To overcome such limitations under climate change, few studies have explicitly calibrated separate SDMs for the juvenile and adult life stage to explore variation in life stage-environment relationships (Figure 2), and even fewer studies explicitly matched stand age to prevailing climatic conditions during establishment. Among these studies, most were concerned with tree species (Supporting Data Table, Zurell et al., 2024). Koide et al. (2016) assessed the spatial overlap of juveniles and adults in an SDM study of *Fagus crenata* in Japan and, by doing so, were able to predict when and where regeneration will decline under scenarios of future climate change. Dobrowski et al. (2015) analysed the niche differences between juvenile and adult SDMs for 62 Western US tree species and found that the recruitment decline depends on the degree of (disturbance-mediated) canopy opening, with closed canopies

buffering some of the climate change effects. Copenhaver-Parry et al. (2020) compared 'naïve' SDMs (describing the adult or unitary niche; Figure 3) with SDMs considering seedling recruitment for five Western US conifers. The study found that inferred niches differed most strongly in the width of the fitted relationships and thus largest uncertainties in predicted environmental suitability occurred at species' range edges. Although examples are sparse in the literature, these few studies illustrate the benefit of explicitly considering demographic stages in SDMs as this allows deeper mechanistic understanding and more nuanced projections, especially for long-lived species and under changing environmental conditions (Jackson et al., 2009).

2.3 | Phenology

Phenology refers to periodic events in the life cycle of species that are typically linked to seasonal and interannual variations in environmental conditions (Figure 1) (Schwartz, 2013). Most plants exhibit distinct phenological stages (e.g. emergence, budburst, flowering, seed maturation, seed dispersal, leaf browning and defoliation) that depend on environmental seasonality and may vary across their geographic range and between years (Figure 4). One

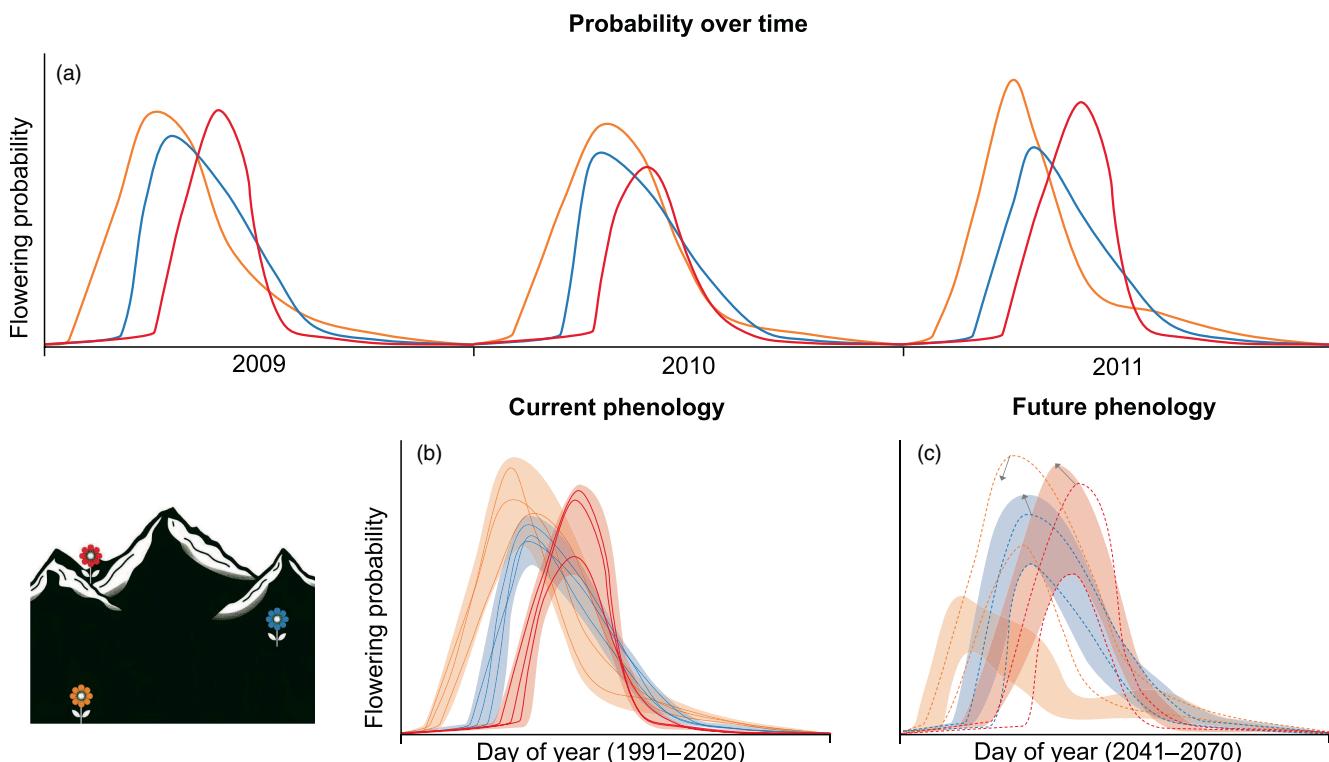


FIGURE 4 Current and future flowering phenology for populations of a hypothetical plant species at three different elevations. (a) The populations show recurring peaks in flowering probability with interannual variations. (b) Phenological assessments may focus on year-to-year differences (identically coloured lines) or on differences across space (coloured polygons). (c) Climate change may induce phenological changes, the impact of which may vary across space. Orange represents a low-elevation population; blue represents a mid-elevation population; and red represents a high-elevation population. Lines are probability curves for individual populations and years; and polygons represent the variation of phenology over a 30-year period.

phenological cycle could last 1 year (e.g. most temperate trees), several years (e.g. cacti), or less (e.g. multiple flowering events per year). It may be triggered by temperature seasonality (e.g. in temperate and arctic regions), in water availability (e.g. in dry tropics) and through interactions between these variables and the availability of nutrients. Phenology has received considerable attention over recent decades as it is a good indicator of climate change (Nord & Lynch, 2009). For example, spring phenology (budburst and flowering) in Switzerland advanced by 30 days since 1985 (Vitasse et al., 2022). Phenological changes can result in cascading effects for entire ecosystems as mismatches in the timing of interacting species (e.g. plants and pollinators) could trigger changes in ecosystem functions and services and thus also affect human well-being.

For SDMs, phenology is relevant because different phenological stages may exhibit distinct environmental tolerances and may also affect the detectability of species. Ignoring phenology may thus bias niche estimates or at least hamper our mechanistic understanding (Table 1). Using the process-based distribution model 'PhenoFit', Chuine and Beaubien (2001) have shown that phenology may be crucial for understanding species range limits. Specifically, their results indicated that towards higher latitudes deciduous tree species are limited by the length of the growing season and the time needed for full seed maturation, while lower latitude range limits were caused by a lack of chilling temperatures that are necessary to break bud dormancy and initiate leave and flower development. As warm range limits are often assumed to be related to competitive effects, the consideration of phenology considerably improved the mechanistic understanding of range-limiting factors (cf. Chuine, 2010). Similarly, Hereford et al. (2017) fitted seasonal SDMs by relating species observations to month and year-specific environmental predictors and found that although predictive accuracy was not improved over conventional SDMs that consider long-term average climatic predictors, their seasonal SDMs allowed improved understanding of the variation of the seasonal climatic niche over space and deriving testable mechanistic hypotheses about limiting factors constraining species ranges.

Climatic sensitivities of different phenological stages have also been intensively researched in the agricultural and horticultural sector. For example, late frost events after budburst can cause significant damage and lead to yield losses, e.g. in grapevines (Sgubin et al., 2018) or sweet cherries (Salazar-Gutiérrez et al., 2014). In agriculture and horticulture, it is thus of economic interest to accurately predict how phenology will change under future climate and how the risk of adverse weather effects will vary across regions in order to adapt management (Miranda et al., 2021). We can directly translate this argument to conservation and suggest that climatic sensitivity of different phenological stages may be relevant for planning priority areas for conservation and management to ensure long-term fitness of protected species.

Another important aspect beside environmental tolerances is that the detectability of species is often tightly linked to their phenological cycle, as some phenological stages (e.g. leave-out, flowering)

are more conspicuous than others. For example, very short-lived species complete their phenological cycles within a few weeks or months and hence may only be observed during specific times of the year (Figure 1). On the other hand, species with very similar morphological traits can be easily confused and might be accurately distinguished only within certain phenological stages (e.g. flowering, fruiting). Thus, the timing of phenological events can directly affect observation bias of species (Table 1) and with that the validity of underlying SDM assumptions (Zurell et al., 2020). In recent years, the digital availability of opportunistic occurrence data provided, for example, by citizen scientists has proliferated (Wüest et al., 2020). Opportunistic data provide a useful source for biodiversity information and can supplement national monitoring schemes. Yet, observation biases and errors tend to be larger in opportunistic data compared to expert monitoring schemes, and it is thus important to consider the sources of uncertainty such as effects of phenology on detectability.

Phenology and demography are tightly interlinked. For annual plants, the annual cycle and life cycle, and thus their phenological stages and demographic stages, are completed at the same time. For longer-lived species, phenology can be informative about the position of a plant's location within its niche. An adult plant will only be able to exhibit a full phenological cycle (including vegetative and reproductive events) if the environmental conditions are suitable. For example, the Chinese windmill palm (*Trachycarpus fortunei*) is an extremely cold-resistant palm species. However, while mature palms can endure substantial frost periods, reproduction is only possible above certain temperatures, meaning that the reproduction niche is substantially smaller than the persistence niche and at some locations adult palms may survive without undergoing a full phenological cycle. These locations are outside of the species' regeneration niche (Figure 3). Of course, we may also find locations where an adult plant may produce seeds, but this does not mean that the environmental conditions are generally suitable for seed establishment. Still, seed production may enhance long-term fitness, for example through a bet hedging strategy. Here, carefully matching the temporal dimensions of environmental predictors and species data is crucial for understanding the species' niche.

3 | METHODS TO INTEGRATE PHENOLOGY AND DEMOGRAPHIC STAGES INTO SDMs

Our literature review yielded only very few studies explicitly considering phenology or demographic stages in SDMs. This quasi-absence of studies could reflect a lack of appropriate data and to a lesser degree outstanding methodological challenges related to computational efficiency. Overall, however, typical SDM tools and workflows can be easily adapted to consider phenology and/or demographic stages. By considering these temporal components of the niche, new and interesting biological phenomena can be studied

and we can gain a more mechanistic understanding of niche and range determinants.

Key to understanding niche variations across phenological and demographic stages is carefully matching species and environmental data. This requires observational data that reflect occurrence of different phenological or demographic stages over space and time, and it requires SDMs that are not only spatially but also temporally explicit, meaning that occurrence data are carefully matched to environmental data at relevant time scales, for example, of specific days or months where a phenological stage was observed or of specific years that match stand age (Figure 1). SDMs have been fitted with data of full spatiotemporal resolution for mobile species (Abrahms et al., 2019; Bateman et al., 2012; Fernandez et al., 2017), but rarely for plants (Hereford et al., 2017). On the other hand, for plants empirical (spatially implicit) phenology models have been used more extensively. These use multi-year time series to investigate the timing of a phenological event in response to environmental variables but are typically restricted to one or few locations (e.g. Rojo et al., 2020; Seghieri et al., 2009), with few spatially resolved examples along elevational transects (Alexander, 2010) or across networks of phenological stations (Jochner et al., 2011; Ziegler et al., 2020).

Methodologically, different model designs could be used to integrate information on phenology and demographic stages into SDMs (Table 2). Spatial and temporal aspects of species distributions may be modelled simultaneously by extending the niche concept to the temporal dimension. Just as species ranges are an emerging property of classical SDMs, species ranges and the timing of occurrence of a specific phenological stage or demographic stage are emerging properties of spatiotemporal SDMs for plants (Box 1; Table 2). Spatiotemporal SDMs for plants may be fitted by matching species observations

with spatially and temporally explicit predictors. For spatiotemporal SDMs of long-lived species, the spatiotemporal predictors should represent years that match the stand age, while for phenology SDMs, the spatiotemporal predictors should represent the time of the year that matches the time of the observation. Opportunistic data often report an occurrence if a single individual of a species is found and reporting of the phenological stage or demographic stage (or age proxy) should be straight-forward. Plot data, on the other hand, report occurrence for several plants within a pre-defined area and may thus contain mixed-age stands and variation in phenological stages. In these cases, we recommend using the youngest age or demographic stage of stands to temporally match predictors and the phenological stage most often observed in the plot, but the effect of such decisions should be further investigated in the future.

Predictors that are temporally variable usually also vary in space, with one important exception. Although we argued above that phenology should be considered an emerging property of environmental conditions, rather than a result of time directly, there is a key environmental factor for plants that is a direct function of time (at least at regional scales): the photoperiod (or simply daylight hours). Beyond a few parasitic species, light is an essential resource for all plants, and daylight hours drive many essential physiological and phenological processes in regions outside the tropics (Flynn & Wolkovich, 2018; Xu et al., 2023). Moreover, in most regions, daylight hours are directly linked to additional, important factors, such as temperature and to some extent also precipitation. Being able to directly deduce information on this essential factor from observation date, for example via sine/cosine mapping (Aodha et al., 2019), or, at larger scales, using the daylight duration formula (Anderson, 2020),

TABLE 2 Overview of types of empirical models to investigate the distribution of species, demographic stages and phenological events.

#	Model type	Response	Spatially resolved data	Temporally resolved data	Output: Distribution	Output: Phenology	Data demand
1	Species distribution model	Species presence/absence	Yes	No	Spatial distribution of species	—	1
2	Empirical phenology model	Timing of phenological event	No	Yes	—	Timing of phenological event	1
3	Stage-specific distribution model	Presence/absence of demographic stage	Yes	No	Spatial distribution of demographic stage	—	2
4a	Spatiotemporal distribution model	Species presence/absence	Yes	Yes (resolution: days, months)	Spatial and temporal distribution of species	Phenology of observation	3
4b		Presence/absence of demographic stage (if life cycle > annual cycles, else 4c)	Yes	Yes (resolution: years)	Spatial and temporal distribution of demographic stage	—	4
4c		Presence/absence of a phenological stage (event)	Yes	Yes (resolution: days, months)	Spatial and temporal distribution of phenological stage	Timing of phenological event	4

Note: Conventional SDMs ignore temporal components while conventional empirical phenology models ignore spatial components. Marrying these two can provide more insights on spatial and temporal variation of niche determinants. The column data demands describes the relative amount of data needed on an ordinal scale.

BOX 1 Case study on the spatiotemporal distribution of the heath spotted-orchid (*Dactylorhiza maculata*) in the Canton of Lucerne, Switzerland

In Lucerne, a canton in Switzerland, blooming individuals of the heath spotted-orchid (*Dactylorhiza maculata*) are most likely observed at intermediate-to-high elevations and in forested areas between June and July. We fitted a Switzerland-wide spatiotemporal distribution model at 100 m spatial resolution with 13 predictors on c. 12'000 observations of the heath spotted-orchid reported to be in full bloom (obtained from the National Data and Information Center on the Swiss Flora) and made daily predictions for Lucerne from April to October of the years 1991 and 2020 (see [Supporting Information S2](#) for full description of data and methods). Habitat suitability for the heath spotted-orchid was consistently high in the southern part of Lucerne, where elevations are higher and typically range between 700 and 1800 m a.s.l. (Figure B1a). At the highest mountain peaks and in the lowlands in the north, habitat suitability was lower, and, in the latter case, suitable habitat was often bound to comparably moist and forested regions. The expected flowering peak (the time of the year of highest predicted probability) varied by more than 1 month across the canton and closely followed differences in elevation (Figure B1b). In correlation with high habitat suitability, the duration of the flowering period also increased at intermediate-to-high elevations, perhaps because the associated cooler average temperatures slow down physiological processes or because small-scale differences in microclimate increase with elevation and terrain complexity, promoting small-scale variations of phenology (Figure B1c).

Recent climate change has left a measurable imprint on the distribution of the heath spotted-orchid, with decreasing habitat suitability for most regions of Lucerne and advancing flowering peaks by 1 day per decade on average. From 1991 to 2020, most regions of Lucerne saw a decrease in habitat suitability of heath spotted-orchid that was most pronounced at intermediate-to-low elevations with medium-level annual habitat suitability (Figure B1d). The slopes of the highest mountains in the canton, on the other hand, experienced an increase in habitat suitability. This redistribution of suitable area towards higher elevations is a commonly observed response to climate change in alpine environments (Rumpf et al., 2018), especially for species that prefer moderate temperatures, as heath spotted-orchid. Besides redistributing, heath spotted-orchid has also advanced and shortened its flowering period. Over the past 30 years, the timing of maximum flowering suitability of heath spotted-orchid advanced consistently, with rates being somewhat higher on the slopes than in the valley bottoms and on flat terrain (Figure B1e). In addition, flowering duration declined in most parts of Lucerne, especially in areas which also saw declines in habitat suitability (Figure B1f). Conversely, the high-elevation regions with increasing habitat suitability usually also saw an increase in flowering duration.

The example of heath spotted-orchid underlines that climate change-induced redistributions of plants are often associated with changes in their phenology. Spatiotemporal models of the distribution of species, demographic stages or phenological stages can simultaneously reveal these changes and provide much more detailed insights than would be possible from classical species distribution models or empirical phenology models alone. This insight is crucial for a detailed understanding of how recent and expected climate change is impacting biodiversity and for well-informed mitigation efforts. Fortunately, with the exponential growth of available biological and environmental data in recent years (Landolt & Bäumler, 2010), such analyses become increasingly more feasible.

allows inference on broad phenological patterns with minimal information (Brun et al., 2024).

In seasonal environments, however, phenology shows substantial year-to-year variation (Vitasse et al., 2022) that can only be resolved with predictors of full spatiotemporal resolution. Among the most relevant factors in this context are daily time series of temperature and precipitation, from which ecologically meaningful statistics, such as growing degree or chill days, can be deduced (Anandhi, 2016; Miranda et al., 2021; Zimmermann & Kienast, 1999). The accumulation interval can be adjusted to shorter periods (e.g. past weeks) or longer periods (e.g. since the beginning of the year), depending on the timing of the phenomenon of interest (Ziegler et al., 2020). Moreover, lag times may be introduced between the timing of the phenomenon of interest and the meteorological statistic considered based on ecological plausibility. Similarly, time series of remote sensing observations may be considered, such as vegetation indices and

other proxies for productivity (Dobson et al., 2023). Compared with classical SDMs, the data demand of SDMs with full spatiotemporal resolution is many times higher, because inference needs to be made across all pixels multiplied by the relevant temporal layers, which makes analyses at large spatial and temporal extents and high spatial and temporal resolutions challenging. Tools such as the recently published R package *dynamicSDM* (Dobson et al., 2023) are very useful in this context, building on Google Earth Engine to efficiently extract information from relevant time series and offering additional useful routines such as spatiotemporal pseudoabsence sampling.

For some plants, spatiotemporal SDMs may offer direct inference on conspicuous phenological events, but for accurate estimates, the phenological stage (or demographic stage) of the observed individuals should be considered, too (Table 2). Brun et al. (2024) found a sound correspondence between the day of maximum observation probability of small, conspicuously flowering forbs and observation

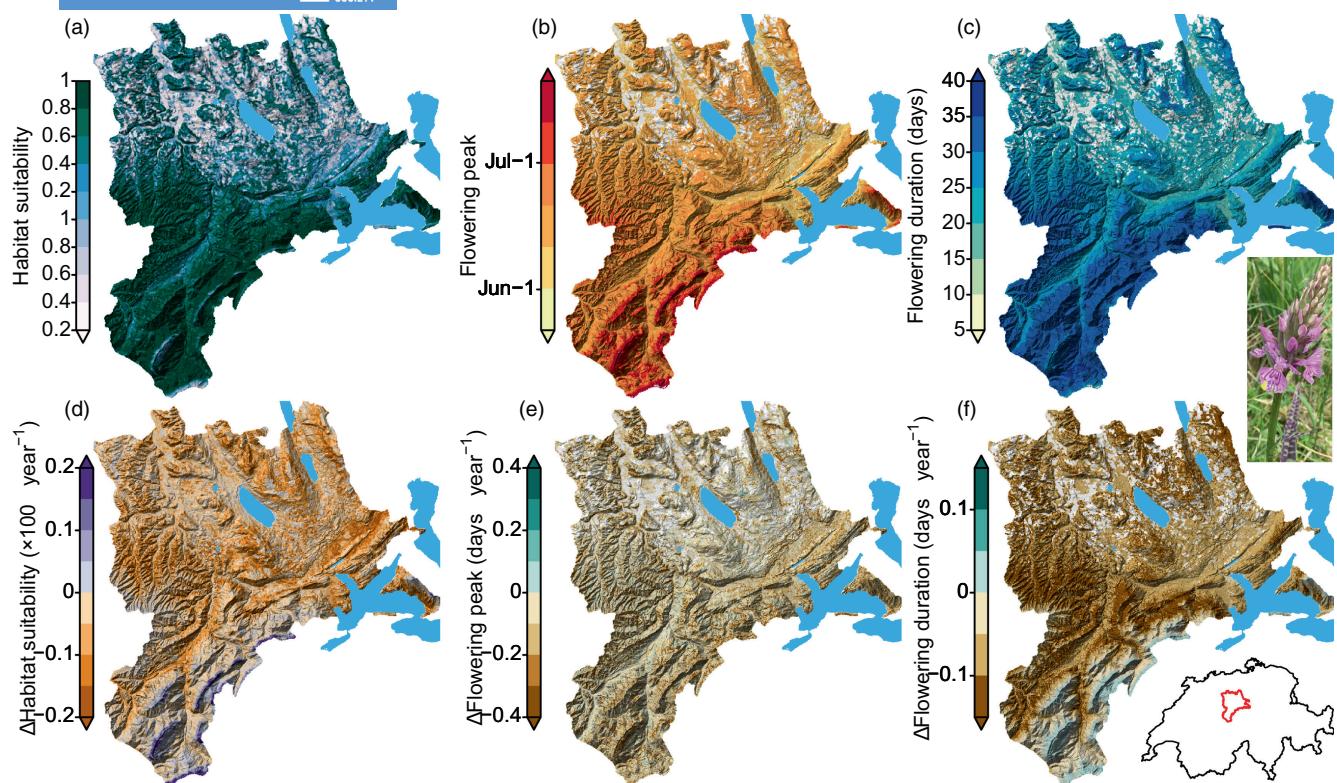


FIGURE B1 1991–2020 means (a–c) and trends (d–f) for habitat suitability and phenology of *Dactylorhiza maculata* in the canton of Lucerne (Switzerland). Habitat suitability (a) was calculated as the 90th percentile of daily (April to October) likelihoods of observation; flowering peak (b) was estimated as the day with maximum likelihood of observation; and flowering duration (c) was calculated as the observation likelihood-weighted seasonal interquartile range. Panels (d)–(e) represent 1991–2020 trends in habitat suitability, peak flowering and flowering duration, respectively. The location of the canton of Lucerne in Switzerland is illustrated on the inset map in the lower right corner, and the appearance of *Dactylorhiza maculata* is shown on the inset on the central right.

dates of individuals that were in full bloom. For most phenological stages, however, such estimates can only be made reliably if they are modelled explicitly. Our literature search identified no published approaches that incorporate phenological stages into SDMs. A straight-forward way of doing so, if sufficient data are available, is filtering species' observations for a specific phenological stage of interest, and modelling it specifically (Box 1; see also Ramírez-Albores et al. (2016) for an example with demographic stages). More sophisticated approaches may be inspired from SDM approaches that discriminate between demographic stages (e.g. Dobrowski et al., 2015).

Different approaches have been proposed to jointly model the distributions of individual demographic stages. In data-limited situations such approaches may be particularly efficient as inference strength can be borrowed across demographic stages. For example, Koide et al. (2016) used a 'size based' SDM to simultaneously model occurrence probabilities of adult and juvenile individuals of Siebold's beech (*Fagus crenata*) in Japan. They used a generalised linear mixed model with presence/absence of both, juveniles and adults, as response variables. The occurrence probability of adults was a function of five climate-related predictors, while the occurrence probability of juveniles was assumed to be a function of adult occurrence probability and snow depth. Similarly, the distribution of juvenile and adult trees has been included as sub-models in hierarchical

Bayesian modelling frameworks (Clason et al., 2020; Copenhaver-Parry et al., 2020).

Although the amount of publicly available occurrence observations has been growing exponentially since global biodiversity databases such as the global biodiversity information facility (GBIF; <http://www.gbif.org>) have been established a while ago (Wüest et al., 2020), they primarily contain information on species identity and spatial coordinates. Conversely, they often lack additional meta information that would be necessary to investigate phenological or demographic aspects. While observation date is more routinely available, phenological stage or demographic stage of the observed individuals is rarely reported. For example, a search of *Quercus robur* occurrence records for the year 2023 in GBIF yielded 24,202 occurrence records with spatial coordinate information. GBIF data contain a metadata field on 'lifeStage' but for *Q. robur* information in this field was only provided for 3% of the records ($n=680$) and contained a mix of phenological and demographic stage information (e.g. adult, flowering, fruiting, seedling and vegetative). Additional information on phenological or demographic stages is vital for stage-specific spatiotemporal SDMs (Table 2) and it would thus be desirable if data portals, for example, for citizen science observations, more routinely ask for such information. Spatiotemporal SDMs could then make use of the dense time series of important meteorological conditions and

remote sensing information that are increasingly available globally, with high spatial resolution (e.g. Drusch et al., 2012; Karger et al., 2021, 2023).

Increased computational power, digital availability of massive amounts of biodiversity data and the proliferation of citizen science approaches offer new possibilities for understanding biological phenomena. Building spatiotemporal SDMs that explicitly account for phenological stages or demographic stages allow a more mechanistic understanding niche and range determinants (Jackson et al., 2009) and can shed new light on the expected plant species response to environmental change (Box 1).

4 | CONCLUSIONS

As climate change is accelerating and affecting virtually all biological processes (Scheffers et al., 2016), we urgently require a deeper mechanistic understanding of the drivers of biodiversity. SDMs constitute a powerful tool in global change ecology and conservation as they allow rapid assessment of species–environment relationships and potential changes in habitat suitability expected under different global change scenarios. Yet, as we have shown here, only few SDM studies explicitly consider temporal components of the niche related to phenology or demography. Ignoring these temporal components in SDMs may lead to biased niche estimates and thus biased predictions into the future. Considering demographic stages in SDMs is particularly important for long-lived species, such as trees, as the temporal mismatch between the reference period of the environmental data (esp. climate) and the regeneration of the plant species can lead to strong over- or underestimation of niche and range margins. At the same time, considering phenological stages is important to gain a more mechanistic understanding of critical niche determinants and for predicting how species redistributions under climate change coincide with or depend on changes in their phenology. This understanding will be vital for assessing future species persistence and resilience of food webs and for informing management and mitigation decisions. Although only few examples of spatiotemporal SDMs exist in the literature to date, novel data such as citizen science data open up new opportunities (Wüest et al., 2020). As we have shown, spatiotemporally resolved SDMs allow detailed insights into spatiotemporal changes in habitat suitability, and the timing and duration of suitable conditions for phenological stages (see Box 1). Similar spatiotemporal SDMs can be constructed for demographic stages. As a prerequisite for such analyses, we recommend that biodiversity databases as well as citizen science portals and mobile apps more routinely ask users to report on phenological stages, and on demographic stages or size. In the future, the collection of such information could also be facilitated by automated interpretation of images supplied by citizen scientists (Wäldchen et al., 2018).

AUTHOR CONTRIBUTIONS

All authors jointly conceived the ideas and designed methodology. Damaris Zurell collected and analysed the Web of Science data,

and all authors equally contributed to the detailed literature review. Philipp Brun conducted the case study analysis. Damaris Zurell and Philipp Brun prepared the figures. Damaris Zurell led the writing of the manuscript with substantial contributions from Philipp Brun and Niklaus E. Zimmermann. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest to disclose.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data table containing the results of the literature search are available in Dryad: <https://doi.org/10.5061/dryad.sn02v6xct> (Zurell et al., 2024). Third party data used in the illustrative example in Box 1 were provided by Info Flora: <https://www.infoflora.ch/en/data/request-data.html>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Literature search.

Appendix S2: Case study on temporally resolved phenological stage SDM.

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