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Review

The importance of including phenology when modelling species ecological niche

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Species distribution models have grown in complexity by incorporating fine-scale variables, including data on microclimate, physiology and species interactions. Recent studies have acknowledged the importance of the spatial scale by including higher resolution maps and more complex climatic variables. However, models rarely consider the consequences of including data related to time. Indeed, species phenology – and potential shifts in phenology due, for example, to climate change – is potentially one of the most neglected aspects of ecological modelling. We present a literature review of relevant phenological aspects at different temporal scales and across several taxa. Such elements should be considered to define better the environmental niche and project present, future and past distribution models. We considered the available studies on plants, insects, reptiles, birds and mammals to evaluate how they dealt with the phenology of the investigated species, as well as the phenology of other resources and interacting species, to infer present, past and future projections. Here we focus on four main phenological aspects that, if not considered, may easily bias any projection, namely: 1) phenology can be accompanied by a shift in distribution within the year (e.g. migratory species); 2) activity may be restricted to a portion of the year (e.g. most ectotherms from temperate climates); 3) survival and reproduction success may depend on the synchrony with other species phenology (e.g. plants–pollinators interactions); 4) changes in climatic conditions can lead to shifts in phenology (e.g. anticipated or delayed blooms or changes in migration timing). In this review, we show how neglecting such factors may quickly lead to project a biased distribution. Finally, we provide a guide on evaluating whether the case study may be affected by such factors and what actions may improve the models.

Keywords: bias, climate change, migration, phenology, species distribution models, species interactions



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Introduction

Species distribution models (SDMs) infer species ranges and habitat suitability by statistically linking known occurrence locations and, when possible, absence locations (Lobo et al. 2010), to environmental data, such as climate or altitude layers (Elith and Leathwick 2009). Such models may associate species presence with environmental variables via correlation (Elith et al. 2011, Peterson et al. 2015) or by explicitly including life-history traits and physiological tolerance to mechanistically link a given species to a set of environmental variables (Kearney and Porter 2009, Peterson et al. 2015). SDMs have become a widespread and valuable tool to make predictions about the potential current distribution of a species (Guisan and Thuiller 2005, Peterson et al. 2011, Guisan et al. 2017), as well as to hindcast the past (Nogués-Bravo 2009, Gavin et al. 2014), or forecast future distribution (Botkin et al. 2007, Kotta et al. 2019).

At the core of SDMs lies the concept of ecological niche, which can be defined as the environmental conditions that a species requires to survive and maintain its populations in a particular space (Hutchinson 1957, Colwell and Rangel 2009). Over the years, the ecological niche has been defined under various perspectives, ranging from broad geographical to local scale and including a functional link with the environment. Grinnell (1924) was the first in using the term 'niche' as the ultimate distributional unit of one 'species or subspecies', while Elton (1927) emphasized the functional species attributes and their interaction within the community. After Hutchinson's work (1957), the fundamental niche was considered the multidimensional hypervolume that encompasses the abiotic factors that limit a species survival and reproduction (i.e. the hypervolume resulting from the intersection of all sets of physiological tolerances). Finally, the realized niche shrinks the fundamental niche by considering the biotic interactions and dispersal barriers (Hutchinson 1957).

Given the complexity in defining the niche of a species (Pulliam 2000), and hence gather the necessary data to model it, one of the most commonly used approaches in SDMs is to consider the climatic component of the niche and to correlate it with known species presence (Kostikova et al. 2014, Gómez et al. 2016, Eyres et al. 2017, Arcones et al. 2021). Most often, local meteorological stations collect the raw climatic data, and several free repositories allow to access them at various geographical scales (e.g. WorldClim, www.worldclim.org/). Some works have incorporated remote sensing data (i.e. satellite imagery), which allow for incorporating complex information like net primary productivity (NPP) or normalized difference vegetation index (NDVI), which are not usually computable from local meteorological stations (Cramer et al. 1999). Such data can be used as a proxy for resource availability or habitat use (Willems et al. 2009, Finstad and Hein 2012), improving the quality of the model predictions (He et al. 2015).

The complexity – and potentially the accuracy – of SDMs may increase by including life-history traits and physiological data, thus potentially strengthening the inference regarding

the projected distribution (mechanistic models, Kearney and Porter 2009). Such an approach is especially promising when applied to changing climate scenarios (Nicotra et al. 2010). The mechanistic modelling approach bears both pros and cons compared to purely correlative methods (Pearson and Dawson 2003). For example, mechanistic SDMs may allow for more realistic projections, especially for ectotherm species. However, mechanistic models are more time-consuming than correlative models and typically require extensive knowledge of the considered species to gather the necessary data (Kearney and Porter 2009).

Regardless of the approach used to model the distribution of a species, the potential effect of phenology is often underestimated or ignored altogether. Phenology studies periodical biological events, and life cycles are modulated by environmental changes throughout the year (Schwartz 2003). Indeed, for many species, the environmental conditions experienced during an early life stage dramatically differ from those encountered later in life (Werner and Gilliam 1984). Also, individuals may migrate within a given life stage, and hence their ecological niche depends on a complex interaction between time and space (Joseph and Stockwell 2000). Similarly, the biotic interactions experienced may vary depending on the life changes, thus further modulating the realized niche (Araújo and Luoto 2007). Finally, climate changes through time and hence considering phenotypic plasticity is paramount (Körner and Basler 2010). As a consequence of such factors, phenology implies that the most important biotic and abiotic variables in a specific life stage may not be relevant during another. Hence, it becomes vital to consider both spatial and temporal dimensions of the occurrence data to consider the whole ecological niche of the species.

In the context of SDMs, the temperature and precipitation often hold a prominent relevance, being among the most critical factors shaping the weather and the climatic niche of a species (Schwartz 2003). Often, species phenological stages are associated with seasonal variation in ecological requirements. The more pronounced environmental seasonality is (i.e. seasonal climatic fluctuations such as winter/summer in temperate zones or dry/wet seasons in tropical ones), the more patent the phenological variation of a species might be. Consequently, a model including yearly average of temperature for a migratory species will likely fail to depict its ecological niche. Similarly, an overwintering species will not experience the meteorological conditions measured by local station and, hence, those data should not be considered. Hence, the biology of the considered species should be examined with care, and the potential effect of phenology on the model may change from negligible to major. Although phenology is one of the main traits that shape organism distributions (Chuine 2010), it has been poorly considered when modelling potential distribution ranges, especially in animals. Indeed, most studies exploring shifts in plant distributions under various climate change scenarios identified phenology as an essential factor for the species' survival (Hereford et al. 2017, Rosbakh et al. 2021). When hindcasting past potential

distribution, phenology is not usually considered, given the difficulty of predicting the past's actual biological stages. Evidence suggests that phenology is a key factor for species fitness, both for animals and plants (Reekie and Bazzaz 1987, Lane et al. 2012) and highly affected by changes in climatic conditions (Körner and Basler 2010, Amano et al. 2014). Indeed, at least for some plants, various models showed that the most important climatic variables vary depending on the considered phenological stage (Chuine and Beaubien 2001, Hufkens et al. 2018). Also, it is common in plant studies to separately model various phenological stages, such as flowering, leaf unfolding and fruit maturation (Chuine et al. 2003, Amano et al. 2014). Unfortunately, most SDM on animal species forgo any potential difference in habitat use, distribution or climatic requirements depending on each species independent phenological seasons or stages.

In this review, we focus on the potential effects of neglecting species phenology in the context of SDMs. Given the enormous array of variation in phenology, we focus on a few selected phenomena, namely migration, overwintering species, species interactions and climate change. We explored how phenology has been considered to study the ecological niche and perform species distribution models. Emphasis is placed on animals, for which phenology has been generally neglected. Given the available literature, here we limit the discussion on terrestrial species, emphasizing vertebrates and insects. These groups have been extensively modelled but include species that vary significantly in the potential effect of phenology on the resulting projections. Because plants models often include phenology, we compare them with animal studies to show the potential effects of including phenology into SDMs. Finally, we provide a scheme summarizing how to improve SDMs in the case phenology plays a relevant role (Table 1), like in the cases we discussed.

Migration

Migratory behaviour is a phenomenon that entails cyclical movement shifts of individuals or populations from one region to another (Dingle and Drake 2007). Such phenomena is widespread across the animal kingdom and has been reported for many taxa (e.g. insects, fishes, marine turtles, birds and mammals, among others), being most commonly studied in birds and some insects (Alerstam et al. 2003, Dingle 2014). In many cases, migration is the consequence of chasing the resource peak of one region while avoiding the decrease in resource availability or harsh climatic conditions in another (Ponti et al. 2018). In most cases, migration occurs twice per year, typically by moving from breeding to a non-breeding ground and vice versa (Dingle 2014). The geographical location of the breeding and non-breeding grounds may be the results of historical factors (e.g. eel reproduction, van Ginneken and Maes 2005) or changing climatic conditions throughout the year (i.e. seasonality). Defining the environmental niche of migratory species implies an extra challenge because they live in different geographic areas and

under different climates during different periods of the year (Fig. 1, top-left panel). As a result, some components of the realized niche may easily differ (niche switching) (Fig. 1, bottom-right panel) depending on the period of the year considered, while other could remain conserved (niche tracking), given the complex biotic and abiotic interactions in different geographical areas (John and Post 2021). For many species, variation in environmental variables may be especially relevant during the breeding season, during which factors like temperature may become critical for successful reproduction (e.g. min temperature for the laying date, Both and Visser 2001).

Several studies that explored the seasonal niche of migratory birds showed that while the climatic conditions could significantly differ between breeding and non-breeding grounds, birds are more conservative regarding habitat selection (Zurell et al. 2018, Dufour et al. 2020, Eyres et al. 2020, Ponti et al. 2020a). Whether migratory species track a specific environmental niche when shifting grounds bears significant consequences on models aiming at predicting their potential ranges. Indeed, most SDMs extract presence data from the breeding grounds and use annual environmental information to proxy climate. In birds' studies, such a protocol has been commonly used to infer both birds' ecological niches and their entire distribution range (Pigot et al. 2010, Cooney et al. 2016), sometimes as a consequence of a lack or bias in the wintering distribution information. However, such an approach may not be appropriate for migratory and non-niche tracking species, likely resulting in biased or overestimated predictions. Nakazawa et al. (2004) showed that even for short-distance migratory birds, it is often not possible to infer one seasonal range using the environmental data of the other, being patent that using only one seasonal area is not enough to determine the whole species ecological niche.

In the review of Eyres et al. (2017), the authors discussed the importance of considering the temporal dimension to determine the climatic niche of migratory birds. Such efforts translate not only in considering the breeding and non-breeding geographical areas but also the climate that species experience in each seasonal range (Laube et al. 2015, Ponti et al. 2020a). Hence, using all-year-round climatic variables may not always be appropriate since it could result in an over- or underestimation of the actual species ranges (Fig. 1, bottom-right panel). Eyres et al. (2017) also pointed out the importance of using this approach for nomadic or short-distance migratory species whenever the climatic conditions vary along the migration axis. Moreover, along with changes in abiotic conditions, breeding and non-breeding grounds typically differ in species assemblages, which will likely affect the realized niche of a migrating species (e.g. tropical areas may have more competitors and higher species densities, Cox 1968). Changes in biotic and abiotic factors may result in substantial differences in fundamental and realized niches that should be considered when selecting the starting data for modelling (Ponti et al. 2020b). For many diurnal birds, insects and other taxa, the timing of migration is monitored, breeding and non-breeding grounds are known and climatic

Table 1. A step-by-step guide to help the modeler including phenology while performing SDMs. The first column refers to the four main systems we discussed in this review. The central columns show the type of data, model approach and result processing to follow when performing SDMs. The rightmost column offers some literature examples of successfully attempts at including phenology into SDMs.

System	Example	Species biology	Data			Model	Projection	References
			Presence/absence	Predictor variables	Model			
Migratory species	Bird migration	Breeding and non-breeding ranges, resident areas, phenology and timing of migration	Occurrence data for breeding and non-breeding areas separately. Consider occurrence point from resident areas as part of both breeding and non-breeding datasets	Environmental data using the months of presence in each area and season: e.g. <i>Milvus migrans</i> : climate of breeding season (Apr–Jul) in Europe–Asia; and climate of wintering season (Sep–Feb) in Africa–SE Asia	Correlative models are the most commonly used	Sum of both projections. Overlapping areas correspond to resident areas	Multispecies birds: Eyres et al. 2017, Ponti et al. 2020b	
	Slow or nomadic migrations		Absence data or background of the whole species distribution area	Monthly environmental data	Independent models for both seasons and areas: wintering and breeding and Monthly independent models.	Sum of projection of each month. Overlapping areas could correspond to transitions areas where species is present in both months	Breeding season of monarch butterflies: Flockhart et al. 2013	
Temperate and overwintering species		Activity season, thermal biology, hibernacula locations	Occurrence data of the activity season, important to have the date information. Occurrence data of the inactivity season (hibernacula) Caution when defining absence data: no detection during no activity season, but presence in hibernacula	Environmental data using the months for the activity and inactivity season independently	Model independently the activity and inactivity season	Using occurrence data without hibernacula information could reflect the potential activity distribution	American black bear: Gámez-Brunswick and Rojas-Soto 2019. Bats: Smeraldo et al. 2018. Lizards: Ceia-Hasse et al. 2014	
					Hybrid models as alternative approach, use correlative models with all occurrence points and annual environmental variables; and mechanistic models (activity season)	Sum of the projections of the activity and inactivity areas/season would reflect the potential species distribution		

Table 1. Continued.

System	Example	Data			Model	Projection	References
		Species biology	Presence/absence	Predictor variables			
Species interactions	Type of interaction: predation, co-dependence, parasitism..., number of interacting species, define the phenophase in which the interaction occurs	Occurrence data with date information of all interacting species	Environmental data corresponding to each phenophases independently. E.g. climatic conditions that induce flowering or fruit maturation; environmental conditions that induce pollinator activity	Model independent phenophases for each interacting species	Overlap in the spatial dimension AND	Monarch butterfly and nectar plants: Kass et al. 2020. Bird-malaria: Gonzalez-Quevedo et al. 2014	
Inferring SDM under climatic changes	Train the model following the steps above depending on the species system	Separate the occurrence points in each species phenophases. Especial focus on where interaction occur	Selection of environmental predictor that define each species occurrence (e.g. variable that define host, vector or pathogen distribution)	Include vector SDM for pathogen-host interaction	Overlap in the temporal dimension (interacting phenophases)	Multitaxon: Parmesan and Yohe 2003. Arctic shorebirds: Arcones et al. 2021. Grizzly bears: Roberts et al. 2014	
					<p>If assuming a phenological time conservation: project the models in the same time interval for each phenophase or season (i) in the future or in the past) than in the present (e.g. wintering season of migratory birds)</p> <p>Potential change in phenological stages: season length or season timing (e.g. flowering months under global warming, or breeding season during LGM)</p> <p>Project the model month per month using past or future environmental variables</p> <p>Sum of all monthly projections and calculate the number of months and the timing interval where the species could potentially occur in each area</p>		

correlates of migrations (i.e. temperature, photoperiod) are recorded. Combining such information allows for better refinement of SDMs (Nakazawa et al. 2004, Eyres et al. 2017, Ponti et al. 2020b).

Modelling cryptic and nocturnal species like bats and some birds still present a significant challenge. Indeed, the migratory patterns of bats and nocturnal birds are relatively harder to record, given the lower detectability and the potential relies on torpor when conditions are unfavourable (Cryan and Wolf 2003). Such life-history traits increase the difficulty of defining many species' breeding and non-breeding ranges and characterizing the most important abiotic variables involved in migration.

Also, some studies suggested that the timings of migration may differ between males and females of bat species as the two sexes may exhibit distinct differences in seasonal thermoregulatory strategies and distributions (Cryan 2003). Other studies showed that intraspecific sexual competition may underlie partial migrations (Chapman et al. 2011). For example, when male density increases in red-spotted newt populations, females tend to migrate while males remain sedentary (Grayson et al. 2011). Hence, studies like Hayes et al. (2015) that consider factors such as sex, timing and geographical distribution are helpful for modelling species that vary in migratory behaviour depending on life-history trait variation. However, it is not always possible to include traits such as sex, because of the challenge of sex identification in many species and the lack of sex information for most occurrence points in public databases (e.g. GBIF).

Unlike birds, which usually perform their migrations in less than two months, insect migrations may involve multiple breeding generations and may require several months before reaching the overwintering grounds (Brower 1995). For example, the well-studied Monarch butterflies require up to seven months to complete their continental migration and reach overwintering grounds in Mexico (Oberhauser and Peterson 2003). This multi-generation migration implies that each generation of butterflies face different environmental conditions depending on the latitude in which they spawn and that they do not migrate to breed but instead breed while migrating (Fig. 1, bottom left and bottom right panel). Dealing with short-life migratory species is extremely challenging, considering that standard tracking devices that inform us about animal movements may not be used. However, other indirect methods such as isotopes analyses could instead indicate the origin of the insect populations (Hobson et al. 2012), and other tracking methods such as tagging techniques could shed light about insect distributions (Urquhart 1941, 1960).

The breeding ranges of many species may change during the year. For example, each generation occurs at different latitudes in some insects before arriving at the wintering range (Holland et al. 2006). Hence, it is essential to consider modelling each period of the migration (e.g. every month) independently, matching the occurrence points and climate for any given time frame (Fig. 1, bottom panels). For example, Flockhart and colleagues (2013) studied the Monarch

butterflies migration modelling each generation independently. Hence, unlike other fast migratory species like birds, the variability in time and space should be considered within seasons when modelling insect distributions. Although non-breeding seasons could be more stable and longer (for monarchs but not for other insects), being possibly modelled as a unique season like in birds, the breeding-migratory season should be treated as a dynamic season with associated differences in time, space and environmental variables.

Many ungulate species undertake seasonal migrations that are modulated by competition or predation and by climate and food availability, typically defined by the wet and dry season in tropical areas and summer and winter in temperate latitudes (Fryxell and Sinclair 1988). In temperate ungulate species, such as the red deer *Cervus elaphus* or the caribou *Rangifer tarandus*, the factors prompting their movements are related to those which limit food availability such as snow coverage (Baltensperger and Joly 2019, Rivrud et al. 2019, Severson et al. 2021). Ungulate migratory movements may also divert or be slower due to human infrastructure, development and activity (Baltensperger and Joly 2019). Human activity also can induce animal movements. For example, wild boars *Sus scrofa* may double their distribution range during the growing season – in comparison with the hunting season – due to the increase in food availability provided by the agricultural practice (Morelle and Lejeune 2015). Hence, for non-flying terrestrial migratory species, the success in performing SDMs could reside in accurately defining the crucial seasonal stages, such as spring and fall migrations, calving and rut (Baltensperger and Joly 2019) and the environmental or anthropogenic factors that induce their movement.

Modelling other migrations such as altitudinal movements should also consider both temporal and spatial dimensions. Species like bats and birds from temperate and tropical regions perform annual movements from lowlands, where they spend the non-breeding season, to highlands, where they live during the breeding season (McGuire and Boyle 2013, Barcante et al. 2017). Although the absolute distance from one altitude to another might be insignificant if considered on a continental scale (typically within less the three or four kilometres), the change in the environmental conditions may be extreme. Again, as for long or short distance migratory species, both seasonal periods (time) and geographical ranges (space) should be considered independently to depict better and model the species' ecological niche (Fig. 1, top-right and bottom-right panels).

Temperate and overwintering species

Temperate and arctic species, such as many insects, reptiles and some mammals, are ideal groups to study the effect of incorporating phenology into SDMs, as their activity, physiology and ecological requirements markedly differ depending on the season considered (Cossins 1987). For many species, the peak of activity concentrates during the warmest months of spring and summer, when the increase

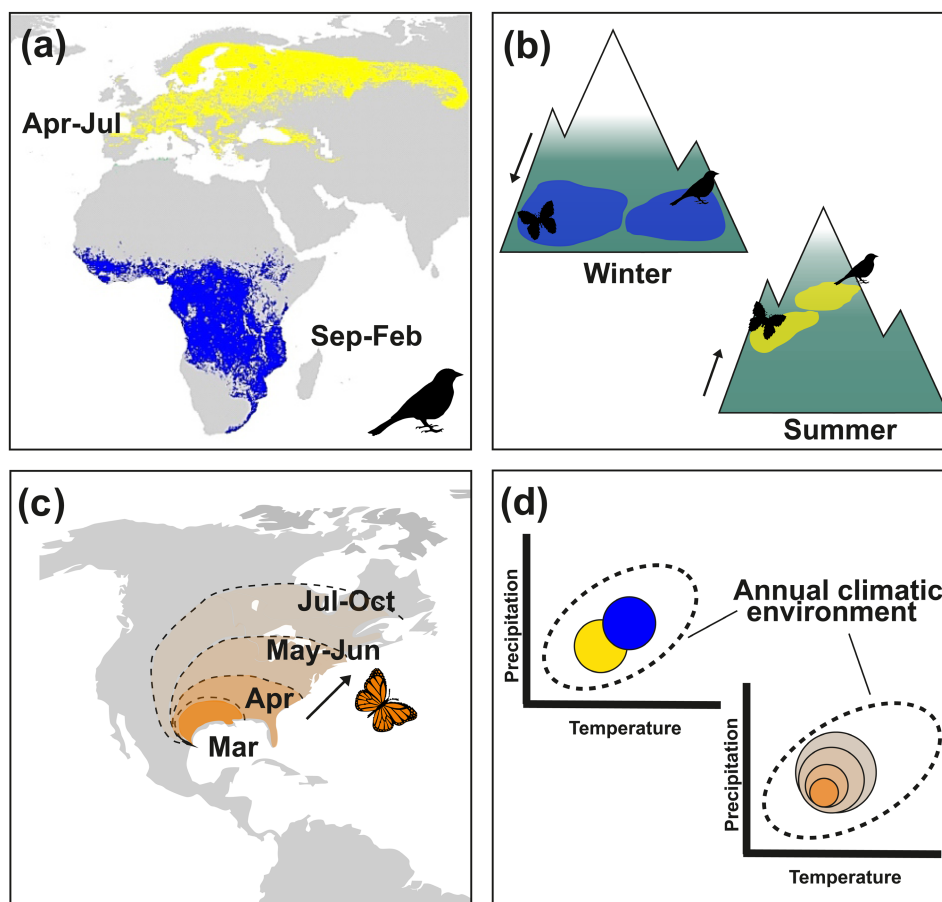


Figure 1. Scheme of the spatio-temporal distribution of (a) a migratory bird species, (b) altitudinal migratory species and (c) monarch butterfly breeding migration. (d) Scheme of potential climatic envelop of breeding (yellow) and non-breeding (blue) seasons of a migratory bird and an altitudinal migratory species, and monthly climatic niche envelop of monarch butterfly breeding season (each circle represents a month or a combination of months). The dotted line represents the potential climatic envelop of the species if considering the annual climatic information instead of the climate corresponding to the months of each season.

in resources and favourable temperatures allow for successful foraging, mating and breeding (Huey and Slatkin 1976, Angilletta 2009). Instead, many temperate species (especially ectotherms) remain inactive during winter, or significantly reduce their activity by spending more time in refuges, lowering the metabolism and heart rate, often in a hibernation state (Cossins 1987, Rial et al. 2010). These strategies allow overcoming harsh climatic conditions, such as low temperatures and decreasing food availability (Lyman and Chatfield 1955). However, such strategies may likely result in a biased prediction for the modeller if phenology is not considered.

For overwintering species such as amphibians, reptiles and some mammals, the challenge of modelling their distribution could be increased by the different environmental requirements of the various seasons. For example, the adequate climatic conditions during spring and summer could be related to the ideal temperature and humidity when food availability increases and promotes a successful reproduction (Hoying and Kunz 1998, Papadatou et al. 2008). Also, most ectotherms will be influenced by the minimum temperature in which the species can be active (Grant and Dunham 1988),

or embryos can successfully develop (Strasburg et al. 2007). Moreover, the probability of surviving winter could be more related to minimum temperature and humidity inside the refuges rather than a minimum or maximum threshold of air temperature, as recorded by meteorological stations (Storey 2006). Ceia-Hasse and collaborators (2014) developed innovative models to infer lizard distributions considering the environmental data and the physiological requirements during the breeding season. These authors performed climatic correlative models, but they also considered the active-breeding season independently. For the breeding season, they used mechanistic models, including the climatic restrictions in the daily activity, which would compromise the presence and persistence of the species. Enriquez-Urzelai and collaborators (2019) combined climatic based models with mechanistic models based on the activity season of the European common frog *Rana temporaria*. This strategy of combining mechanistic and correlative models (hybrid models) could have the potential to better depict the distribution of many species, given that it embraces several biological mechanisms and processes at different scales (Tourinho and Vale 2022). In European

bats, [Smeraldo et al. \(2018\)](#) found that the variables defining the ecological niche in summer and winter differ significantly, which became essential to determine which conditions could limit their distribution range. The authors highlighted the importance of including the occurrence points considering the temporal dimension to avoid under-representing actual species distributions. For example, if only data from the summer season were included, the projection overestimated the species presence in the southern part of the distribution while underestimating the northern grounds where the species actually overwinter.

When working with overwintering species, the modeller should consider the temporal bias in the occurrence data, due to the limited detectability of species during the overwintering season. For example, most distribution information on temperate reptiles relies on detecting individuals during the spring–summer active season. Although snakes' hibernacula, for example, are well known in some areas ([Rudolph et al. 2007](#), [Luiselli et al. 2018](#)), the dimension of presence data from both seasons is not comparable. This approach could result in a model reflecting the potential activity map rather than the actual distribution of the whole year. As a result of such an observation bias, the forecast may overestimate the potential distribution of a species ([Strasburg et al. 2007](#)). In this context, when using presence–absence data to perform SDMs, phenological information should be considered when defining absence points. Indeed, no detection using sampling methods like transect observations or camera-traps ([Sollmann 2018](#)), may not reflect true absence ([Mackenzie and Royle 2005](#)). Also, when pseudo-absences are defined as the points lacking suitable climatic or habitat characteristics for a given species ([Lobo et al. 2010](#), [Barbet-Massin et al. 2012](#)), authors should consider that unsuitable conditions may differ from one phenological stage to another.

As for migration patterns discussed in the previous section, modelling an overwintering species considering the temporal dimension may help build a more accurate projection of species range. For example, [Gámez-Brunswick and Rojas-Soto \(2019\)](#) modelled the distribution of the American black bear monthly. The resulting projections showed the areas where the bear is active each month instead of the yearly distribution range. Hence, how representative the distribution map will be for the winter season depends on the ability of the species to move and the use of different areas in both seasons. It is known, for example, that bats use different roosts in summer and winter, with the subsequent climatic difference ([Smeraldo et al. 2018](#)). In any case, fragmenting the SDMs to account for the seasonal activity of a species may yield useful biological insights. For example, it could inform about the minimum length of time needed for a species to survive and reproduce before hibernations, which, in turn, may be affected by climate change (see the last section).

Further, to better fit SDMs, the modeller should include the environmental conditions that reflect the ecological requirements of the species ([Guisan and Thuiller 2005](#)). In species with such pronounced phenological patterns, it is necessary to include the environmental variables that define the

seasonal and life-stage ecological niche ([Ponti et al. 2020a](#)). For example, the adults of a particular reptile species could have an ample climatic tolerance range, but the thermal range for egg development and growth may be more restricted, limiting the spatio-temporal distribution of the species ([Kearney and Porter 2009](#)).

Species interactions

Most studies performing SDM rely on the climatic envelope to model a species. However, climatic variables represent only a fraction of the actual ecological niche of the species. Several authors have proposed new methods that integrate pairwise biotic dependencies and other biotic interactions in the models, improving them more than using only abiotic data ([Ovaskainen et al. 2010](#), [Sebastian-González et al. 2010](#), [Kissling et al. 2012](#), [Wisz et al. 2013](#)). Including biotic interactions may become especially important when modelling species that depend strongly on other species to survive or reproduce (e.g. feeding specialists, [van Asch and Visser 2007](#)). Indeed, in the case of feeding specialists, the distribution range will depend on the interaction between suitable climatic conditions and prey distribution.

Moreover, as discussed in the previous sections, phenology and synchrony become important when performing SDMs involving interacting species. Unfortunately, most models assume a constant relationship between space and time, which may easily bias the projections if species interactions occur only during specific phenophases. For example, if a pollinator is modelled alone, SDMs may propose a particular area as suitable. However, if the flowering of the pollinated plant is not synchronous with the pollinator activity in the projected area, the model prediction will likely be biased ([Donnelly et al. 2011](#)).

The most common studied interspecific interactions and potential distribution projections focus on plant–insect or parasite–host dependency ([Singer and Parmesan 2010](#), [Giannini et al. 2013](#)). Among plant–animal interactions, the dependency may happen at different times of the year or change during ontogeny. For example, some plant–animal interactions change over ontogeny, with some herbivorous insects becoming pollinators when adults ([Yang and Rudolf 2010](#)). Plants and insects often present defined phenophases, such as flowering and fruit maturation in plants and diapause, reproduction or metamorphosis in insects. Such phenophases should be modelled independently as submodels, given that both biotic and abiotic factors likely differ in each phase.

The dependency and interactions between species can be mutual or directional. Both species may depend on each other (e.g. symbiosis), or only one species may depend on the other (e.g. specialized predator–prey, [Elzinga et al. 2007](#), [Kharouba et al. 2015](#)). In other cases, a species may depend on more than one species to sustain its population densities and distribution range. For example, the acorn woodpecker's distribution in the US is limited by the diversity of oak species, where areas with a single oak species become unsuitable

for this bird (Koenig and Haydock 1999). The complexity increases in tropical communities like those inhabiting the neotropical cerrado savannah, where the interactions may occur in multitrophic systems with at least three interacting trophic levels – plants, herbivorous (Lepidoptera) and herbivorous predators (ants) (Oliveira and Freitas 2004). Although most of the studies that incorporate species interaction consider both plant and animal spatial distribution (Araújo and Luoto 2007, Preston et al. 2008, Schweiger et al. 2008, 2012), only a few include the environmental characteristic of the critical phenological stages (Kass et al. 2020). Like Correa-Lima et al. (2019), some studies explored the potential distribution of bird or insect-pollinated plants, including flowering timing information but not the potential distribution of the bird or insect species they depend on. Kass et al. (2020) used a very innovative approach to estimate monarch butterflies' distribution in Mexico during the overwintering season. They included both biotic and abiotic factors, using climatic data and nectar plant distributions incorporating the phenological information by considering only the flowering stage of nectar plants with which monarch butterflies interact.

Similar to models performed considering plant–animal interaction, animal–animal interactions have been incorporated in some SDMs (Giannini et al. 2013, Gonzalez-Quevedo et al. 2014, van der Mescht et al. 2016, McDonough and Holloway 2021). Among animal–animal interactions stand out the parasite–host ones. The common cuckoo *Cuculus canorus*, a brood parasitic species, and its hosts represent an excellent example of parasite–host interactions in which the phenology plays a determinant role. The cuckoo's and its hosts' arrival to their breeding grounds – and the overall breeding season – should overlap to assure cuckoo's reproduction (Saino et al. 2009). Other parasites (such as some pathogens) depend on a species vector to infect their host. In these cases, the modeller should consider the vector phenology and its distribution when performing SDMs. For example, to model the probability of prevalence of a blood endoparasite species in a bird species, the pathogen's distribution, the vector (e.g. mosquito species) and the host (e.g. bird species) should overlap in space and time (MacDonald et al. 2020). Furthermore, suppose this infection would happen only in the breeding or wintering grounds of a migratory species. In such a case, the breeding or wintering season of the species should coincide with the phenology of the vector.

Commonly, authors modelled the potential prevalence of an endoparasite by using environmental data that predict the distribution of the vectors, as these kinds of pathogens depend strongly on them (Gonzalez-Quevedo et al. 2014, MacDonald et al. 2020). Considering phenology in SDMs became of paramount importance when inferring the pathogen's prevalence, given that the suitable spatial–temporal window of host–vector–pathogen interaction could change under climatic oscillations (Sehgal 2015). Although several studies have investigated the role of the phenology in interspecific interactions for several taxonomic groups (Bartomeus et al. 2013, Kharouba et al. 2018), this information is still omitted

in most SDMs. Hence, including this information would likely enhance the accuracy of current SDMs and help identify the critical phenological stages for the survival and persistence of the studied species.

Climate change

Past and current climatic changes have affected and are still shaping species distributions and phenological timing (Stefanescu et al. 2003, Kharouba et al. 2014). Several studies have reported species responses to current climate change, which may involve spatial displacements and advancements or delays of certain phenological stages (Parmesan and Yohe 2003, Root et al. 2003, Parmesan 2007, Lebourgeois et al. 2010, Fig. 2). The distribution of other species remains stable, showing no apparent phenological response to climatic changes (Parmesan and Yohe 2003). The phenological responses vary with latitude and taxonomy, being stronger and faster at higher latitudes (Post et al. 2018) (in both hemispheres) and in some taxa (e.g. amphibians compared to groups such as trees or birds, Parmesan 2007).

Climatic changes may have a higher impact on those species whose phenology changes only at some life stages but not others. This scenario may be the case for several long migratory birds that anticipate their laying date due to the increased temperatures and food availability in the breeding grounds. However, if birds do not anticipate the arrival to their breeding grounds sufficiently, the breeding success may be endangered (Both and Visser 2001, Saino et al. 2011). The lack of plasticity in some ecological traits due to physiological or genetic constraints may cause such a mismatch (Gienapp et al. 2007, Pulido 2007, Møller et al. 2010).

When performing SDMs and predicting phenological changes under climatic changes, the modeller typically assumes a scenario of ecological niche conservatism (Pearman et al. 2008). Under such an assumption, the species will shift spatial distribution or adjust its phenology to track climate change (Parmesan and Yohe 2003, Root et al. 2003, Fig. 2). How exactly each species will respond depends on many factors, including dispersal ability (Kim et al. 2020), physiological tolerance (Chefaoui et al. 2019) and the potential for adaptation to novel conditions. For example, plants are typically more prone to adjust their phenology over a short period rather than shifting their distributions, given their limited dispersal ability (Amano et al. 2014).

As a result, it is challenging to infer future and past distributions of species potentially able to change their phenology. Moreover, if phenology changes throughout ontogeny, each life stage is likely associated with different ecological requirements. In such a case, each life stage should be modelled independently. For example, Woods (2013) performed independent SDMs to unravel the potentially suitable areas for the larvae and eggs of the tobacco hornworm *Manduca sexta*, considering that the two stages differ in thermal tolerance. Moreover, the presence of certain climatic or ecological conditions in an area becomes essential, together with the

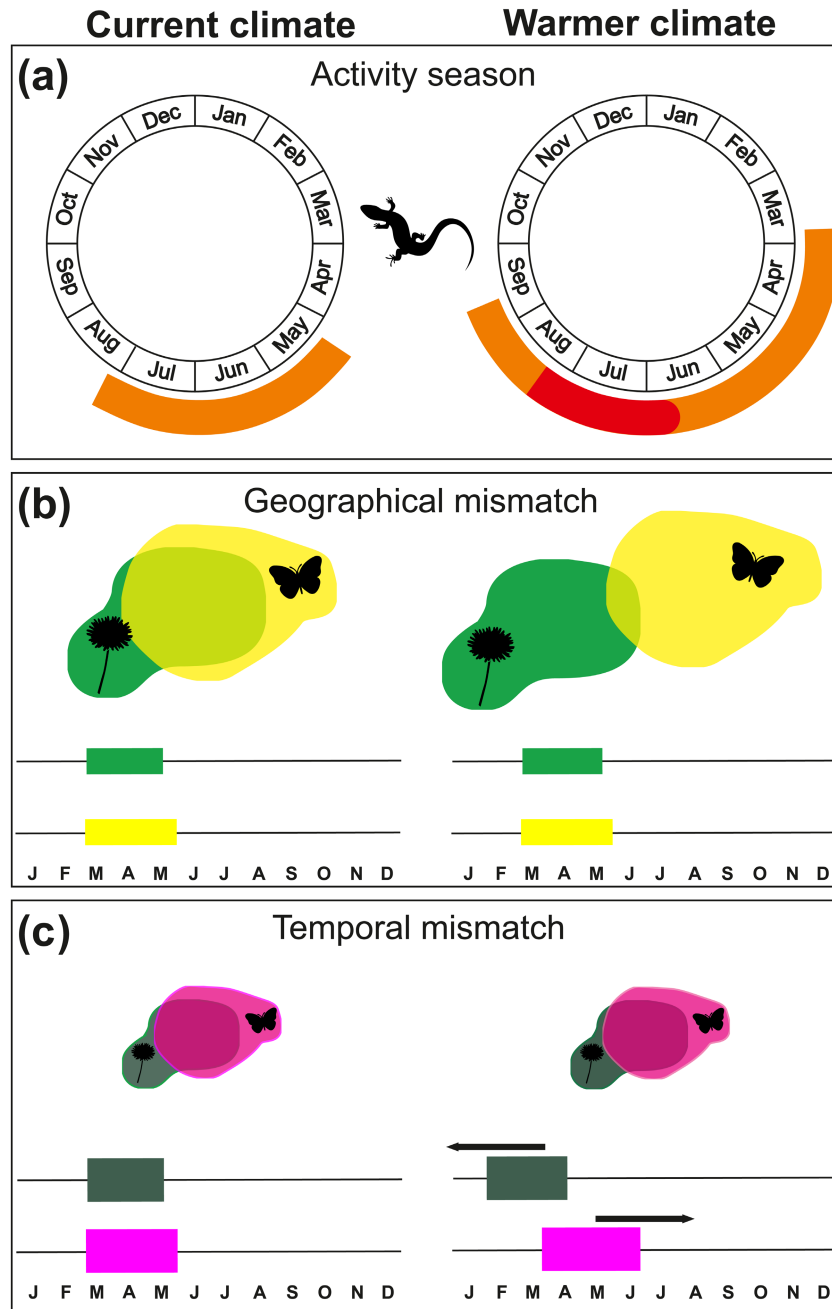


Figure 2. Scheme of potential changes in distribution and phenology of different species under a warming scenario. (a) Duration of the active season of an ectotherm (in orange). In red is represented the warmest period which would compromise the activity of the species. (b) Potential changes in spatial distribution of two species: a plant and a pollinator insect. Plant distribution in green and insect distribution in yellow. The bars correspond to the phenological stage when both species interact; flowering (in green) and appearance of the pollinator insect (in yellow). (c) Potential changes in phenological timing of a pollinator insect (magenta) and the flowering stage of a plant (dark green).

duration of such conditions. For example, migratory birds' breeding season usually lasts between two or three months (Moltofte et al. 2007, del Hoyo et al. 2018). The suitable conditions for breeding should be present during the period studied for those consecutive months that would allow the reproduction and survival of the species. This approach was used by Arcones et al. (2021), who inferred the breeding

distribution of Arctic birds during the last glacial maximum. The annual mean conditions, in this case, may not be enough to detect the continuity of suitable conditions during the whole phenological stage or season. Such an approach is also helpful to predict if breeding season may expand or contract due to future or past climatic changes which could, in turn, prompt a change in migratory behaviour. For example, the

non-prediction of suitable areas in the breeding range during the breeding season could indicate a loss of migration (Zink and Gardner 2017), or a latitudinal shift in the predicted distribution may suggest a reduction of bird migratory distance (Ponti et al. 2020b). In the case of migratory bats, climatic changes may not only affect the timing of migration and migratory distance, but also the duration of the hibernating season (Sherwin et al. 2013). In such a scenario, distribution modelling may face an extra challenge, as the phenology of both the activity season and migration could be affected by environmental shifts.

A rapidly changing climate may affect the timing for activity, reproduction or growth and may reduce or increase the reproductive season or the activity season, which could compromise the survival and persistence of species. For example, ectotherms represent a particularly vulnerable group to climate change because their physiology, including growth, locomotion and reproduction, depend directly on environmental temperature (Angilletta 2009). The increase in temperature in cold and temperate latitudes could positively affect some species, such as insects and reptiles, as their activity season becomes longer and the window for reproduction increases (Deutsch et al. 2008, Ljungström et al. 2015, Rutschmann et al. 2016). Besides, the distribution of mountain-dwelling ectotherms may change as the climatically suitable time-window at higher altitudes may lengthen (Sheldon et al. 2011). However, for species that already experience warm seasons, an increase in temperature may limit the activity during the hottest months, resulting in a reduced or bimodal activity (Deutsch et al. 2008, Sinervo et al. 2010, Levy et al. 2016, Fig. 2, first panel). Also, tropical and temperate species often differ in their thermal tolerance. Temperate species generally experience a broader range of environmental temperatures throughout the day and the year, while tropical ones, which evolved in habitats characterized by more stable conditions, tend to have narrower thermal tolerances (Janzen 1967, Deutsch et al. 2008). Although mountains could represent an opportunity to escape from rising temperatures, montane tropical species could have less dispersal ability to shift their altitudinal distribution than temperate ones (Janzen 1967). Although mechanistic SDMs may add valuable insights when inferring any species distribution, they become significant for ectotherms, as their thermal tolerance heavily affects their potential distribution (Pontes-da-Silva et al. 2018). For example, the length of the activity season of a lizard species will be determined by the operative temperature range and the water loss tolerance. As a result, hotter and drier seasons will likely affect ectotherms distribution (Sannolo and Carretero 2019). For such reasons, it becomes essential to consider the duration of certain climatic conditions and physiological tolerance when modelling ectotherms.

As a response to climatic changes, shifts in phenology can cause disruptions in the synchrony of ecological interaction (Visser and Both 2005, Kharouba et al. 2018). The case of species that depend strongly on other species to feed, such as specialist butterflies (Diamond et al. 2011),

or bears from temperate latitudes which need very caloric food (Roberts et al. 2014, Gámez-Brunswick and Rojas-Soto 2019), represent extra-challenge cases for SDMs. In such cases, if the shifts in phenology go in the same direction for both species, there may be a negligible effect on SDMs. However, species react differently to climatic changes in most cases, confounding the potential effect of phenology shifts on SDMs (Visser and Both 2005, Thackeray et al. 2010, Fig. 2, second and third panel). For example, Roberts et al. (2014) used an integrative approach to infer the grizzly bear suitable habitat under a climate change scenario. The authors modelled the 17 most consumed plant species by grizzly bears, projecting their suitable future areas during spring and summer when bears are active. However, it should be considered that uncertainty and over/infra-prediction derived from each modelled plant species might in turn increase the uncertainty about the projected distribution of the focal species (the grizzly bears).

Also, the duration of the interaction between species may increase or decrease depending on how environmental conditions affect both species. For example, under a global warming scenarios, Arctic and alpine ecosystems would be highly affected by the change in seasonality (e.g. the advance of snow melt) which may have an effect on species interactions (Ernakovich et al. 2014). The alteration in plants phenology and the increase of the available time for vegetation growth could affect the equilibrium of plant species composition. As a results, the interaction with herbivorous species may be altered, for example by reducing the available time for foraging on high-quality leaf matter, or by changing herbivorous migration timing (Sturm et al. 2005, Rickbeil et al. 2019). Finally, long term data series may allow detecting the tendency of a species under climatic changes. For example, this has been done for several tree species (Badeck et al. 2004), strengthening the projection regarding species' future responses to climate change.

Conclusions

The in-depth knowledge of the biology and ecology of a given species is critical to obtain realistic and accurate models for species distributions (Zurell et al. 2020). In this review, we showed that several life-history aspects across a variety of taxa might significantly affect the performance of any given SDM. Taking into account phenology allows the researcher to get more sound results, potentially closer to the actual distribution of a species and more accurate and realistic future and past projections. We focused on four general aspects. First, the niche of migratory species may vary in time and space. The common practice of using breeding sites to extract presence points and annual climatic variables (e.g. in European birds) may easily bias SDMs predictions. Instead, SDMs should consider both the breeding and non-breeding grounds and timing of slow-paced migrators (as in the case of butterflies). Second, the fundamental niche of temperate species may dramatically differ depending on the considered life stage. Extreme conditions experienced during

winter and summer may significantly affect both adults and larvae or eggs survival, and accounting for such conditions may significantly contribute to better forecast distributions. Third, despite the distribution of all taxa being partially affected by biotic interactions – resulting in the realized niche – the survival and reproduction of some taxa heavily depend on such interactions. It may be beneficial to model a multi-species scenario in parasitic interactions or specialized feeders rather than limiting the inference solely on the species of interest. Finally, the ecological niche heavily depends on climatic factors, which vary in time. Data suggests that animal and plant taxa differ in the degree of niche conservatism or potential to acclimation or adaptation to new climatic conditions. Hence, explicitly accounting for such plasticity – or lack thereof – may likely results in better inference on the present, past or future distributions. Generally speaking, several authors showed that combining a purely correlative approach with a mechanistically driven one often results in a better model. They are encouraging researchers to include life-history traits and physiological data in their inference as much as possible, given the extent of benefit that may result from such an integrative approach.

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Data availability statement

No new data were created or analyzed in this study.

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