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A review of the methods for studying biotic interactions in phenological analyses

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Abstract:

1. Phenological events play a key role modulating ecosystem services; however, the complex and interlinked nature of ecosystems means interactions among different taxa during phenological events can have consequences for the entire ecosystem. Currently, there is a lack of a unified criteria on the methodologies studying phenology and biotic interactions.

2. We performed an extensive integrative review of works evaluating phenology and biotic interactions. We identified four broad categories of studies that have explored biotic interactions within phenology research: 1) spatial and temporal asynchronies, 2) biotic factors as covariates, 3) simulation studies, and 4) interaction indices.

3. We found that spring phenology has received much more attention than any other seasons, while mutualistic and obligated interactions, as well as trophic interactions and networks have been explored more routinely than facilitation or competition. Authors tend to interpret co-existence among species as biotic interactions without any direct measurement of these, particularly in spatial and temporal asynchrony studies, but this also occurs to a certain extent in all categories. We also found a lack of formal examination in most studies exploring phenological mismatches in response to climate change.

4. We propose a conceptual framework for the inclusion of phenology in the study of biotic interactions that apportions research into the conceptualisation and modelling of biotic interactions. Conceptualisation explores phenological data, types of interactions, and the spatiotemporal dimensions, which all determine the representation for biotic interactions within the modelling framework, and the type of models that are applicable.

5. Finally, we identify emerging opportunities to investigate biotic interactions in phenology research, including spatially and temporally explicit species distribution models as proxies for phenological events and the combination of novel technologies (e.g., acoustic recorders, telemetry data) to quantify interactions.

Resumen:

1. Los eventos fenológicos juegan un papel fundamental regulando los servicios ecosistémicos, la naturaleza compleja e interconectada de los ecosistemas conlleva que las interacciones entre diferentes taxones durante eventos fenológicos puedan tener consecuencias sobre el ecosistema en su conjunto. Actualmente no existe un criterio unificado sobre las metodologías de estudio de la fenología y las interacciones bióticas.

2. Hemos desarrollado una revisión integrativa extensiva sobre artículos cuyo objetivo era evaluar fenología e interacciones bióticas. Hemos desarrollado cuatro amplias categorías en las que se pueden agrupar los estudios que han explorado interacciones biológicas en estudios fenológicos: 1) asincronías espaciales y temporales, 2) factores bióticos como covariables, 3) estudios de simulaciones, 4) índices de interacciones.

3. Nuestra revisión muestra que los eventos fenológicos que tienen lugar durante la primavera han recibido mucha más atención que la fenología de ninguna otra estación, así como el hecho de que las interacciones y redes tróficas han sido exploradas más frecuentemente que interacciones de facilitación o competencia. Los investigadores tienden a interpretar coexistencia entre especies como una interacción biótica, sin que haya una medición directa de dicha interacción, en especial en los estudios de asincronías espaciales y temporales, aunque ello también ocurre a cierto nivel en el resto de las categorías. Además, también hemos encontrado una falta de examinación formal en la mayoría de estudios que exploraron desajustes entre eventos fenológicos en respuesta al cambio climático.

4. Proponemos un marco conceptual para la inclusión de la fenología en el estudio de las interacciones bióticas que divide dicho estudio entre la conceptualización y el modelado de las interacciones bióticas. La conceptualización explora el tipo de datos fenológicos, tipo de interacciones y las dimensiones espacial y temporal, todo ello determina la representación de las interacciones bióticas a lo largo del modelado, así como el tipo de modelos aplicables.

5. Por último, también identificamos oportunidades emergentes para la investigación de interacciones bióticas en fenología, incluyendo modelos de distribución de especies temporal y espacialmente explícitos usados como representaciones de eventos fenológicos, así como el uso combinado de nuevas tecnologías (por ejemplo: grabadores acústicos o datos procedentes de telemetría) para cuantificar interacciones.

Keywords: biotic factors, coexistence, mismatch, phenology, species interactions

1. Introduction

Phenology is the study of cyclic and seasonal phenomena in organisms, such as leaf unfolding and senescence, flowering of plants, migration events, and timing of the breeding season (Forrest & Miller-Rushing, 2010; Mayor et al., 2017). The outstanding impacts that phenology exerts in the functioning of ecosystems and their services are well established and have fostered much research in recent decades (van Schaik, Terborgh & Wright, 1993; Peñuelas & Filella, 2001; Peñuelas, Rutishauser & Filella, 2009; Timberlake, Vaughan & Memmott, 2019; Duchenne et al., 2020). Some of these main phenological impacts include the carbon sequestration potential of ecosystems (Le Quéré et al., 2017) with variations in net carbon uptake (Keenan et al., 2014) and carbon regulation (Richardson et al., 2009; Brzostek et al., 2014). Thus, phenology plays a key role in modulating ecosystem processes.

The complex and interlinked nature of ecosystems means that changes in the abiotic components (e.g., climate), might alter the cues that phenological events follow (e.g., temperature or photoperiod), which could lead to advanced or delayed phenological events in one or more interactor species (Forrest & Miller-Rushing, 2010). Shifting phenologies among different taxa can display direct

or indirect impacts on biotic interactions (Wolf, Zavaleta & Selmants, 2017). For example, earlier flowering time that overlaps with other plant species could expose plants to lower pollinator activity (i.e., direct impact) as a result of competition, while also resulting in reduced herbivory pressure, which has a subsequent effect on fruit onset (i.e., indirect impact) (Vilela, Del Claro, Torezan-Silingardi & Del-Claro, 2018). The sensitivity of biotic interactions and interaction networks to climate change means that many species and ecological networks could experience decoupling or losses of interactions, which could have potentially long-standing consequences for the entire ecosystem and its services (Oliver et al., 2015).

The phenological response to climate change drivers has been explored for many taxa, particularly for plants. Earlier flowering and leaf unfolding in spring as a result of climate change are well documented (Primack, Higuchi & Miller-Rushing, 2009; Rafferty & Ives, 2011; Mayor et al., 2017; Mohandass, Campbell , Chen & Li, 2018). However, not all organisms respond in the same way. For example, within a plant community some species might experience noticeably earlier flowering as a response to variations in climatic factors, whereas other species might show low impact or remain unchanged (Vilela et al., 2018). This can result in phenological mismatches at different trophic levels (Fig. 1a,d, e.g. flowering time and pollinator activity; bird migration and insect development), thus threatening biodiversity because of differences in phenological sensitivity to climate (Thackeray et al., 2016; Kharouba et al., 2018). These phenological mismatches have been proven to be particularly important for supressing specialized interactions, where higher trophic levels depend on a reduced number of species in the lower levels (Both, Van Asch, Bijlsma, Van Den Burg & Visser, 2009).

The interactions between plant and pollinator are usually asymmetric, where a plant species depends strongly on an animal species (pollinator), but the animal depends weakly on the plant (and vice versa) (Bascompte, Jordano & Olsen, 2006). Asymmetric interactions usually occur within (predominantly) nested networks, allowing both generalist and specialist plants to interact with both generalist and specialist pollinators and thus maintain the ecosystem (Schweigher et al., 2010). Therefore, in the case

of (local or global) extinction of one of the interactors or asynchronies between partners, the network could buffer the effect of such events, but there would be uncertainties related to how resilient species might be to such changes (Fig. 1b,e). Moreover, many species initiate phenological events based on species interactions, with many aphid species initiating migration based on the senescing of host plants (Dixon & Glen 1971; Watt & Dixon 1981), which may or may not be captured by changes in the abiotic conditions alone (Holloway, Kudenko & Bell, 2018). In addition, the effect of climate change can disrupt biotic interactions in many ways, for example, turning from a favourable scenario of facilitation to competitive exclusion or competence (Blois, Zarnetske, Fitzpatrick & Finnegan, 2013) or by advancing or delaying phenology of species that exhibit changes in their interaction types through ontogeny, which is where species shift their relationship from competition to predation, facilitation to competition or herbivory to mutualism during their life cycle (Yang & Rudolf, 2010), illustrated in Fig. 1c,f. Despite the complex network of interactions operating in ecosystems, the role of phenological shifts on species interactions, and vice versa, remain poorly understood (Sargent & Ackerly, 2008; Varpe, 2017). In a recent study, Morente-López, Lara-Romero, Ornosa and Iriondo (2018) documented a great variation of within-season interactions in a plant-pollinator network in which modularity (strength of groups of interacting species) was greatly influenced by species phenology. Thus, evaluating the role of phenology in species interactions is vital for a better understanding of biotic interactions and ecological networks.

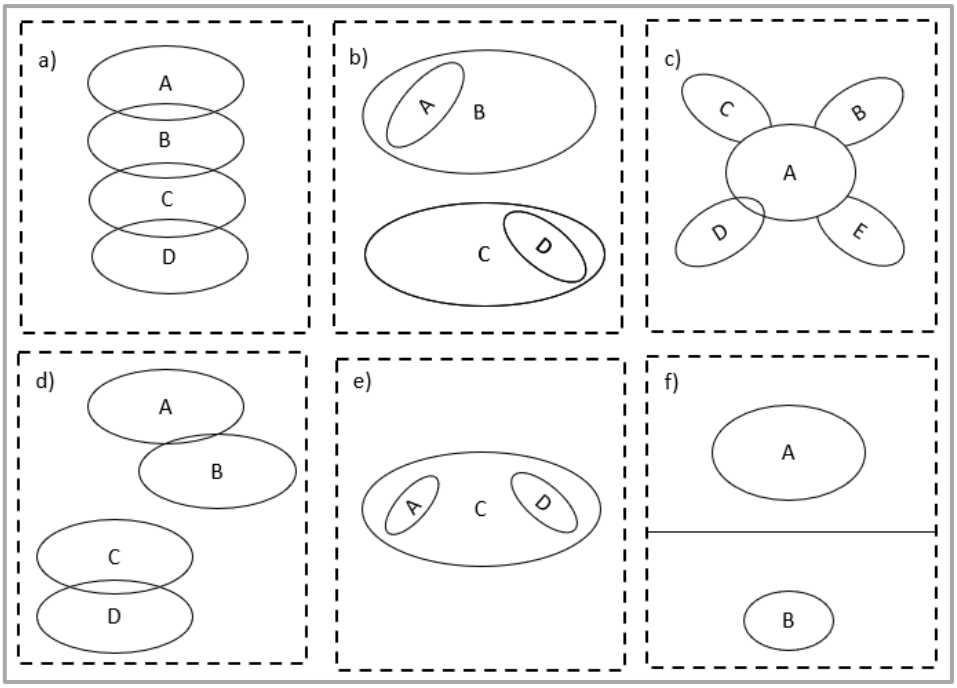


Figure 1. Conceptualisation of biotic interactions under normal conditions, i.e. matching phenologies, among different trophic levels (a,b,c) vs phenological mismatches (d,e,f) caused by an imbalance in the ecosystem, i.e., climate change or fragmentation. a) Species (A, B, C, D) interaction through the trophic network, where A interacts with B, who interacts with C, who in turn interacts with D. b) Representation of obligated interactions (A+B), (B+C) where species A depends on B and species D depends on C. c) Species A favouring through facilitation, under favourable conditions or a particular stage of its ontogeny, by providing nutrients, refugia or resources, the occurrence of species B, C, D and E. d) Interaction decoupling as C and D advanced their phenology while B delayed it and A remained constant as result of a perturbation, i.e. temperature rise. e) A+B interaction lost after a perturbation, i.e. habitat modification or climate change, hence A now depends on C, exerting pressure on both C and D. f) Facilitation turned into competition in where A excluded all species and reduced available space for B through competition.

There are several challenges when incorporating biotic interactions in phenology research, which may have impeded its development. Firstly, there is a lack of information regarding many species interactions, and even when information is available there is often a lack of replication that makes it difficult to extrapolate the methodologies and results across species, environments, and models (Baselaga & Aráujo, 2009). The high complexity of biotic interactions and the mechanisms involved in the build-up of interaction networks, makes it difficult to model them statistically, being typically parameterised in models as proxies of presence-absence of interactor partners (Palacio & Girini, 2018). Similarly, many interactions are unknown, hindering evaluation of biotic interactions for many species (Atauchi, Peterson & Flanagan, 2018; Morente-López et al., 2018), and furthers the use of

subjectively defined proxies. Finally, biotic interactions are also dynamic in nature; however, they have typically been evaluated during just one part of the life cycle (e.g., spring), assuming that interactions are static in space as well as time (Bateman, Van Der Wal, Williams & Johnson, 2012).

Therefore, biotic interactions have been relatively neglected in phenology research (Elzinga et al., 2007; Morente-López et al., 2018) despite the important role they play in life cycle events. Consequently, developing a generalised framework for the incorporation of biotic interactions in phenology research has been difficult, meaning studies addressing interactions among different species and trophic levels are rare. While methods have been proposed to investigate species interactions in phenology research, these have often arisen in disparate fields, with a predominant focus on quantifying temporal mismatches in relation to the abiotic conditions. By not implementing measures of biotic interactions in phenology research, models ignore one of the most important ecological processes that can modify, disrupt, or decouple phenological events across ecosystems.

In this review we aim to investigate the methodologies used to evaluate the effect of phenological change in biotic interactions and address the main challenges derived from the study of these complex relations. This review aims to identify important gaps of knowledge, explore different approaches of studying biotic interactions within phenology research and provide future directions, all pivot questions for integrative reviews (Sayer, 2018). Details of the methodology used to undertake the review and the list of studies within an initial Web of Science keyword search are presented in Supplementary Information 1. Studies that have explored biotic interactions within phenology can be broadly grouped into four main categories: 1) spatial and temporal asynchronies, 2) biotic factors as covariates, 3) simulation studies, and 4) interaction indices. Through this we review, we aim to create a generalised framework for the incorporation of biotic interactions in phenological research. Finally, we end our review by exploring emerging opportunities that could be employed to investigate biotic interactions within phenology research, and subsequent challenges arising from these new methods.

2. Spatial and Temporal Asynchronies

Asynchrony among species in phenology research has predominantly focused on variations in climatic factors (e.g., temperature, precipitation) that are the common drivers of phenological events of many taxa, consequently leading to spatial and temporal mismatches between interlinked species (Yang & Rudolf, 2010; Thackeray et al., 2016; Mayor et al., 2017). Most studies investigating temporal mismatches in phenological events have focused on monitoring climatic induced changes of a single species or an array of species over an extended temporal period (e.g., 30 years) that are usually linked through the trophic network (Gordo & Sanz, 2006; Jones & Creswell, 2010; O'Neil et al., 2012; Dunn & Moller, 2014). For example, fluctuations in bird migration trends, arrival dates, and laying dates have all been documented in relation to decades of variation in temperature and precipitation in wintering grounds and spring breeding areas (Gordo & Sanz, 2006; Jones & Creswell, 2010; Dunn & Moller, 2014). However, studies typically rely on the assumption that earlier emergence or arrival to breeding grounds will result in the mismatch of interactions that are not evaluated or quantified in any way.

Advancements on incorporating biotic interactions within studies investigating temporal mismatches have systematically modelled the relationship between species (Gordo & Sanz 2005; Burkle, Marlin & Knight, 2013). For example, Gordo and Sanz (2005) used a temporal series of phenological events of plants and pollinators including date of flowering and pollinator emergence over a 50-year period in order to infer decoupling of plant-pollinator interactions. Climate induced changes in plant phenology were estimated using dimension reduction models (e.g., two dynamic factor analyses) to identify common temporal patterns within plant phenological events. Advancing on this, the authors employed regression analyses to determine patterns of change on the timings of phenological events (e.g., insect emergence, bird migration) showing advancement on insect emergence related to advanced flowering but the interaction among both was not explicitly analysed. Figure 2a highlights a hypothetical visualisation of such results, with the fitted line representing a linear model for showing

185 the trend on timing (asynchronies) of two phenological events, plant flowering and insect emergence.
186 The dotted line represents documented differences in Julian days between the two studied
187 phenological events, extracted from independent datasets, and evidences the lack of direct method
188 for the evaluation of biotic interactions in previous research.

189 Biotic interactions are frequently inferred as species co-occurrence in time rather than documenting
190 them directly in the field. However, Rafferty and Ives (2011) evaluated the timing of flowering blooms
191 using t-tests to determine significant advancements on flowering over time, categorising plants into
192 two groups; advanced flowering and unchanged due to climate change. By recording presence of
193 flowering and visitation, they tested whether phenological mismatches among plants and pollinators
194 could be a limiting factor on pollination for both groups of plants. Visualisation of these records using
195 a contingency table (Fig. 2b) provides a clear representation of which species are (significantly)
196 mutualistically interacting.

197 Thus, temporal mismatches in phenological events are frequently used as proxies of biotic
198 interactions, i.e. egg laying date and peak abundance of main food source as proxies for predator-prey
199 interactions (Visser, Holleman & Gienapp 2006; Mayor et al., 2017). Usually those changes in
200 phenology or interactions are then statistically tested by the application of linear regression models
201 where the explanatory variables are the interaction between two species, measured as the
202 coexistence of interactor partners over time and space, i.e. presence or absence of species A and B in
203 a place during a particular time period, or a phenology event of one or more species. For example,
204 studies have regressed differences in the timing for which phenological events of mutualistic or
205 obligated interactors occur during a given period (Hegland, Nielsen, Lázaro, Bjerknes & Totland, 2009;
206 Saino et al., 2009; Rafferty & Ives 2011; Bartomeus et al., 2011). For instance, Mayor et al. (2017)
207 investigated how the phenological intervals between green-up and bird migrant arrival changed for
208 48 breeding passerine species in North America, identifying both positive and negative changes in
209 phenology (Fig. 2c). Interestingly, they highlighted instances where positive values of the phenological

interval were given because migrants arrived earlier, tracking advances in vegetation phenology. Conversely, negative values in phenological intervals corresponded to migrants showing advanced or unchanged phenology while vegetation phenology was delayed. Surprisingly, they found that even when migrants arrived earlier following trends in green up, they did not keep pace adequately with it. Additionally, the phenological interval varied throughout ecoregions, suggesting the important role geography may play in phenology.

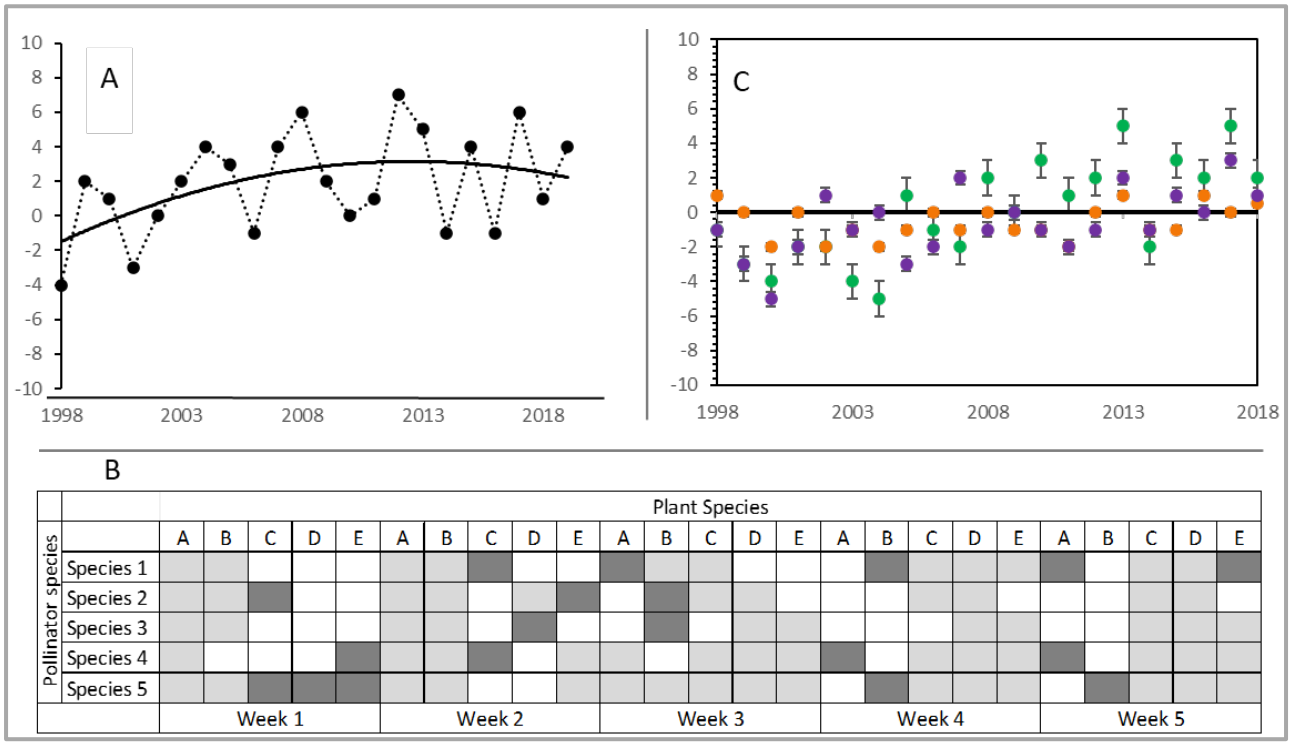


Figure 2. Different approaches to modelling biotic interactions from proxies. A) Modelled elapsed days between date of insect emergence and flowering date for an insect and its main flower resource, showed in calendar days (Y axis), over a decade (X axis), adapted from Gordo and Sanz (2005). Black dots represent positive or negative differences between timing on phenologies of the two taxa, dotted line reflects trends in variations of temporal asynchronies, fitted line represents a linear model of the tendency of these asynchronies. B) Conceptualization of an experimental network of plant-pollinator interactions over time in which an assemblage of plants (species A, B, C, D and E) was manipulated to evaluate the role of changed vs unchanged flowering timing, adapted from Rafferty and Ives (2011). i.e. A, and B manipulated to flower earlier than their current mean flowering date, C and D manipulated for a delayed flowering and E remained unchanged according its current flowering date. Pollinator visits (species 1 to 5) are documented over time, light grey squares represent plant-pollinator interactions and dark grey squares represent low rate pollinator visitation. C) Trends of phenological change, in comparison to mean (0), estimated by number of calendar days per year (Y axis) for three phenological events: green up (green dots), date of arrival of a migrant bird species (orange dots) and date of an insect emergence (purple dots), over a decade (X axis), bars indicate standard error.

Phenological advance corresponds with positive values over the mean while delay in these events are represented by negative ones, adapted from Mayor et al. (2017).

Application of temporal asynchronous analysis requires long-term time-series data, and due to the resources required to collect such data, this research is often restricted spatially to very localised sites. Subsequently, studies are beginning to use species distribution models (SDMs) to quantify spatial and temporal asynchrony in phenology. SDMs use information regarding the locations of organisms together with geospatial environmental parameters to identify species-environment relationships and use these to extrapolate habitat suitability into novel space and time (Elith & Leathwick, 2009). While phenology has not been a traditional application of SDM research, in part due to their static representation of a species niche (Peterson et al., 2011), studies are beginning to emerge (Porfirio, Harris, Stojanovic, Webb & Mackey 2016; Yun, Lee & Yoo, 2020). For example, Yun et al. (2020) modelled the distribution of the cuckoo (brood parasite) and 12 passerine birds (host species) to ascertain the amount of spatial overlap in their distributions under changing climates. By quantifying the difference in spatial area, the authors identified a decrease in suitable habitat for all species, but also a decrease in the amount of overlap between cuckoos and their hosts, subsequently impacting breeding phenology.

Therefore, the need for a spatial consideration in any phenological research investigating asynchrony among species is key, as changes in timing may occur differently across ecoregions, ranges, and altitudes. For example, Benadi, Hovestadt, Poethke and Blüthgen (2014) used an altitudinal gradient as proxy for expected climate change over time, to evaluate the degree of synchrony between specialised flower visitors and their main plant resource. By modelling plant-insect phenological shifts among different altitudes with linear mixed-effects models, the authors demonstrated that consistency of specialised pollinators and phenological synchrony with their main source was not maintained at different altitudes.

Studies investigating spatial and temporal mismatches among species have generally focused on spring phenology (Visser et al., 2006; Primack et al., 2009; Mayor et al., 2017; O'Neill et al., 2012;

Bartomeus et al., 2011; Phillimore, Leech, Pearce-Higgins & Hadfield, 2016), while studies addressing autumn phenology are scarcer (Gordo & Sanz, 2005; Gordo & Sanz, 2006; Gallinat, Primack & Wagner, 2015). Although evidence of advanced spring phenology is widespread (Heghland et al., 2009; O'Neill et al., 2012; Phillmore et al., 2016), this trend is unclear for autumn phenology and the lack of comparative studies makes it difficult to discriminate patterns during this season (Gordo & Sanz, 2005). Moreover, in many of the aforementioned studies, interactions were considered to be static among species, as well as expected to change linearly with the abiotic conditions. The expected linear change in such cases is realistic until some point, but species will not advance their phenology endlessly. Thus, the nature of relationships, such as type and strength, might change along with abiotic conditions, meaning the selection of parameters need to be appropriate to the system under study in order to account for such factors (e.g., non-linear relationships - Austin, 2007). Consequently, under the current climate change scenarios (IPCC, 2018), phenological mismatches have the potential to deeply impact biotic interactions, therefore long-term spatially and temporally explicit phenological studies could help to improve management actions to preserve the integrity of interaction networks.

3. Biotic Factors as Covariates

Despite their relevance, biotic factors have been relatively neglected in phenological studies, particularly when compared to the historical use of abiotic drivers (Thackeray et al., 2016; Wolf et al., 2017); however, studies have begun to incorporate them as additional explanatory variables or covariates in statistical models. Biotic variables are often included in the models to investigate the role of species interactions on phenological events, predominantly using data obtained from manipulative field studies (e.g., visual identification among transects, capture-recapture, and monitoring of nests - Visser et al., 2006). Generally, interactions through trophic levels are documented more often since impacts on one of the interactors of these obligated or specialised networks, in which one species directly depends on other as a food source, will lead to a response on the other partner. For example, by evaluating differences in the onset of forage species (either herbivores or predators), the impact

of any phenological mismatch in the reproductive success of forager populations can be estimated (Visser et al., 2006; Post & Forchhammer, 2008). These manipulations aim to account for the effect of temporal or spatial changes in environmental conditions, phenological events or biotic interactions. For example, Martin and Maron (2012) tested the effect of reduction in snow cover, given a 25-year period of snowfall decline, as a factor influencing bird and plant population declines through increased herbivory and nest predation. The authors studied changes in plant assemblages for herbivory-prohibited (i.e., simulated snow cover) and herbivory-exposed sites finding that reduction in snow cover exposed plant assemblages to higher herbivory pressure, leading to declines in bird populations due to increased nest predation. However, an increase in plant and bird populations (including a reduced nest predation) was documented in herbivory-prohibited areas.

Research has also addressed the importance of the spatial dimension of phenological shifts. For example, larger shifts in phenology (e.g., longer mismatches in Julian days) have been related to higher latitudes and elevations, which act as a proxy for increases in global temperature (Chmura et al., 2019). Altitudinal gradients serve to illustrate climate change effects as conditions in upward populations are usually associated to pre-climate change scenarios while downward populations serve as example of the conditions that upward populations would experience in the future (Alexander, Diez & Levine 2015). Although some of the reviewed studies monitored biotic parameters, there is still a marked importance of abiotic factors, with studies typically testing several within models i.e. factors such as temperature increase and nutrient enrichment on specialised trophic interactions (Lu, Siemann, Shao, Wei & Ding, 2013; de Souza Laurindo, Gregorin & Tavares, 2017; Terraube, Villers, Poudré, Varjonen, & Korpimäki, 2017). For example, Terraube et al. (2017) showed the importance of climate factors and forest management on the foraging success of an owl species by using field data and GLMMs. The authors documented a trend of decreased prey biomass stored in nests related to increasing rainy days and days with frost, which in turn is expected to affect the biomass and fitness of the target owl species. However, despite the importance of incorporating both abiotic and biotic factors on interactions, few experimental studies have actually tested this within a phenology context.

Alexander et al. (2015) exposed plants to different treatments of abiotic conditions and presence of expected interactor species in order to determine if competition or facilitation would dominate plant assemblages under predicted climate change. By using mixed-effect models and GLMs, the effect of presence of competitors on the transplanted individuals was estimated, showing that under warmer conditions the identity of the competitor had a significant effect on the transplanted individuals' success. Wolf et al. (2017) carried out experiments manipulating biodiversity of plant assemblages to reflect random or realistic biodiversity loss, in terms of the number and identity of species. Their aim was to test for the effect of biotic interactions on the timing of flowering peak (highest flower abundance per species and plot were used as a surrogate variable for time of flowering) of each species. In this case, plots with low plant diversity showed earlier flowering, while flowering peaks between species were more dispersed in high diversity treatment plots than in monocultures. Other studies have begun to test both abiotic and biotic factors in experimental settings (Bresson, Varoquaux, Bontpart, Touraine & Vile, 2013; Koyama & Tsyuzaki, 2013), with studies manipulating environmental conditions useful to determine changes in phenology and the evolution of specialized interactions under predicted climate change conditions. Moreover, experimental works manipulating abiotic and biotic conditions in order to evaluate phenological response and adaptive success are performed by translocating individuals (usually plants) to new areas (within and beyond) their distributional range, or through lab manipulation (Lau & Lennon 2012). Thus, the inclusion of biotic interactions in phenology research could change the statistical response, effect, and importance of abiotic variables.

Despite these advancements, many studies lack any direct measurement of biotic interactions. For example, Merrill et al. (2008) documented the distributional range shift of a butterfly related to elevation on its lower distributional limit and to the absence of host plants at their upper distributional limit. Since the target butterfly needed the presence of any of the host plants for completing different stages of their life cycle (i.e., phenology), the lack of host plants at higher elevations was assumed to be responsible for determining the butterfly's upper distributional limit, despite there being no direct

measurement of their biotic interaction, taking host plant presence as a proxy. Similarly, Kass et al. (2020) used presence of resource and refugia providing plants at a monthly resolution, aiming to capture the importance of plant phenology on the distribution of the monarch butterfly during autumn migration, with co-existence records serving as a proxy to infer suitable habitat for the butterfly.

Conversely, there is usually a lack of replication in most field or manipulative studies. For example, even when biotic interactions are statistically proven to be one of the main explanatory variables within a system, the lack of replication over time and the scarcity of comparative studies might lead to misinterpretations. For instance, Theobald, Gabrielyan and Hillerislambers (2016) demonstrated the importance of pollinator-mediated seed production of a montane plant species. The authors tried to investigate the role of pollinators for determining the range limit of the plant (through pollen limitation), suggesting the importance of different pollinator groups for reproductive success; however, factors determining the species' range limit could not be separated from plant interannual variations. Further, some studies evaluate small populations which highlight the fact that small sample sizes might mask the effect of other possible factors and lead to erroneous interpretations (Post & Forchhammer, 2008; Benadi et al., 2014). Furthermore, although most of these experimental studies include environmental variables, given the scale and dimension of these open mesocosm experiments, there might be environmental variables that are not considered and could explain some of the statistical variation found in them (Wolf et al., 2017), compounding our ability to interpret such biotic interactions within these models. In addition, most of the studies address spring phenological events monitoring weather conditions during the growing season neglecting winter climate change conditions that are of great importance for the phenology of plant and pollinators (Makoto et al., 2014).

4. Simulation models

Simulation models are statistical models where one or more parameters are manipulated in order to elicit predictions in the response of the ecological factor under consideration (Chuine & Régnière, 2017). These factors could include the presence or abundance of a species, the spatial or temporal changes of a particular phenological event, and the persistence of a biotic interaction. These models have been used to explore a wide array of phenological events, such as co-occurrence of interactor species influencing pollination interactions (CaraDonna et al., 2017), the role of plant-pollinator synchrony in community assemblages (Bartomeus et al., 2013) and the role of changing phenology on population trends (Dunn & Moller, 2014). Although simulations exploring the responses of species under climate change are common in ecology (Keith et al., 2008; Virkkala, Heikkinen, Leikola & Luoto, 2008; Dullinger et al., 2012), during the development of this review we found very few papers where simulations investigated the effect of climate change on phenological events or biotic interactions (Memmott, Craze, Waser & Price, 2007; Araújo, Rozenfeld, Rahbek & Marquet, 2011; Roberts, Tansey, Smithers & Phillimore, 2015; Bateman et al., 2016; Goberville et al., 2016; Schleuning et al., 2016).

Simulation models have been used to predict the evolution of ecological networks, by modelling predicted phenological mismatches among interactor partners, as well as extracting interactor species from modelled networks to determine extinction effects when one or more species are removed (Memmott, Waser & Price, 2004; Memmott et al., 2007). By modelling extinctions in mutualistic networks, species sensitivity to climate change driven coextinctions can be estimated. For example, Schleuning et al. (2016) modelled the effects of climate change on ecological networks, and subsequently simulated secondary species extinction as a consequence of the sequential loss of plant and animal species. Network sensitivity was then quantified ranging from no secondary species going extinct to all species. Simulations showed that specialized animals would suffer greater impact than plants from secondary extinctions in mutualistic networks due to climate change. Moreover, applications of simulation models can be used to construct networks of co-occurrences that serve as

proxies of interactions or to infer biotic interactions from co-occurrence patterns (Araújo et al., 2011; Araújo & Rozenfield, 2014). For instance, Araújo and Rozenfield (2014) created a point-process model from co-occurrences to infer biotic interactions and to evaluate their relevance at different spatial scales. Spatial overlap (attraction or repulsion) together with probability of occurrence of interactors in space was interpreted as a signal of biotic interactions that were scored according to the number of times species co-occurred within cells in order to estimate their spatial importance. Their results suggested that the effect of negative interactions was clearer at fine scales and diluted at coarse scale whereas positive interactions (mutualism, commensalism) and those related to consumer-resources were scale independent.

Simulations have also been useful to model species distributional limits and probability of survival beyond geographical ranges. For example, Benning, Eckhart, Geber and Moeller (2019) used field experiments to train simulations on plant fitness in the presence and absence of herbivory. Simulations were tested by exploring the impact of herbivory on the fitness and survival of a Californian annual plant species, investigating delayed phenology and the probability of survival beyond its geographic range. When climate conditions were advantageous (i.e. higher precipitation) simulations showed that probability of survival and fitness of the species at their range limit and beyond was much higher when the effect of herbivory was moderate than when this antagonistic biotic relationship was excluded, although not high enough to support population establishment and growth. While this study explored antagonistic interactions, mutualistic interactions within networks, such as pollination, were addressed the most frequently across all simulation studies (Memmott et al., 2004; 2007; Bartomeus et al., 2013; Schleuning et al., 2016).

Few studies employed mechanistic models such as physiologically based weather-driven demographic models (PBDMs) aiming to incorporate phenology and biotic interactions while also accounting for abiotic parameters and multitrophic population dynamics (Ponti, Cossu & Gutiérrez, 2009; Ponti et al., 2013). Further, recent approaches using simulations to explore phenology have shown that such

models can be used to predict the probability of detecting pairwise biotic interactions through the use of occurrence data and detectability of species, estimation of probability of interactions, and connection of interaction networks (Graham & Weinstein, 2018).

However useful simulations are, these approaches face similar challenges, such as the lack of robust data on interaction networks, as well as sensitivity to the lack of knowledge about rare interactions (Olito & Fox, 2015). In many cases, the lack of basic knowledge on species biology and biotic interactions could lead to erroneous predictions or interpretations that under- or over-estimate the power of these models (Memmott et al. 2007). Additionally, considering a network of interactions as a sealed system is often a caveat of these methodologies. For example, when modelling species extinctions, these models are performed assuming that no new interactions are entering the system, which can undermine the power of the model as this is not entirely realistic. Moreover, despite the importance of phenology structuring networks of interactions (Morante- López et al., 2018), studies modelling biotic interactions frequently ignored the phenological dimension of these (Araújo et al., 2011; Araújo & Rozenfield, 2014; Schleuning et al., 2016). Although there are some advances in the field of predictive models of biotic interactions, in particular the novel approach of Graham and Weinstein (2018) to develop models predicting species interactions, the lack of a robust methodology on this topic limits the use to elaborate predictions on species interactions.

5. Interaction Indices

Interaction indices have been used to measure the degree of interaction among species, with research focusing on synchrony among interactor species (Donoso, Stefanescu, Martínez-Abraín & Traveset, 2016; Oleques, Overbeck & de Avia, 2017), interactions within communities (Buxton, Brown, Sharman, Gabriele & McKenna, 2016; Molina-Venegas et al., 2016; Oliver et al., 2018), and interactions as a network (Junker et al., 2013; Robinson, Losapio & Henry, 2018). For example, Benadi et al. (2014) evaluated local specialisation of insect on flower morphology, calculating two indices (d') and (H2') to estimate the level of specialisation on pairwise and interaction networks, respectively. Both indices

compared the number of visits of a pollinator (later pooled to taxonomic groups) to a plant species, and then further comparing visits to total flower resources and a null model of expected visits. The authors demonstrated different degrees of specialisation among taxonomic groups of pollinators and the importance of floral traits (tube length) rather than plant species identify.

Novel advances on field monitoring of phenology, particularly using new technology, are leading to the development of community interaction indices (Buxton et al., 2016; Oliver et al., 2018). For example, Buxton et al. (2016) used a novel acoustic index, developed by Pieretti, Farina and Morri (2011), to monitor spring and winter phenology of songbirds. The acoustic complex index (ACI) measures the vocalizations produced on an avian community and poses as an important tool for the study of phenological events at large spatiotemporal scales. This index is calculated as the differences in sound pressure level among adjacent seconds of the recorded period divided by the total value of sound pressure level for the recorded band. Acoustic recorders were placed in different areas in order to acquire different ACI values over a three-year period. ACI values were compared with species-specific acoustic analyses to determine changes in the acoustic landscape produced by the arrival of migrant birds. Further, the relationship between species beta-diversity and ACI was documented with differences in values among seasons calculated through Bayesian change point analyses and GLMMs. Abrupt changes in phenology were recorded in spring, but these were not as prominent during the autumn season, partially due to extreme weather events obscuring the acoustic data. Thus, potential of acoustic recorders to continually monitor the phenological landscape offers a unique insight in measuring how phenology (and subsequent biotic interactions) change over time (Deichmann et al., 2018), and while several novel challenges are associated with the technology (Shonfield & Bayne, 2017) their use offers a means to establish a holistic monitoring system that can integrate both local and global data to phenology research (Buxton et al., 2016).

Junker et al. (2013) investigated plant pollinator networks using two interaction indices to account for functional individual traits (S_i) and multiple traits (V_i) structuring pollinator niche-breadth while also

456 evaluating the effect of plant phenology. They expected that individual flower traits of different plants
457 visited by the same taxon would have lower Euclidean distance between them than those that do not
458 share visitors. To investigate this hypothesis the authors calculated the individual trait width index (S_i)
459 that employed distance matrices, weighted means, and random distances (among other parameters).
460 Simultaneously they created the trait volume index (V_i) exploring groups of flower traits that could
461 influence pollinator preferences, calculated as the product of all individual S_i of each tray by each
462 volume V_i for each taxon as a measure of taxon specialisation. The authors demonstrated that
463 specialist pollinators showed no restrictive morphological traits to access nectar resources and were
464 influenced by plant phenotypes, whereas generalist pollinators showed no preferences across a suite
465 of traits.

466 **6. Proposed conceptual framework**

467 Phenology has developed within disparate fields, including ecology, geography, physiology, chrono-
468 biology and genetics, meaning there has been a wide variety of viewpoints in how to address this
469 phenomenon (Visser, Caro, van Oers, Schaper & Helm, 2010; Pau et al., 2011). Moreover, biotic
470 interactions are complex; they change over time, assemble and decouple by processes such as
471 turnover, and depend on many factors such as modularity (strength of sets of interactions), climate
472 change, local extinctions and presence of invasive species (Schweiger et al., 2010; Schleuning et al.,
473 2016; CaraDonna et al., 2017; Morante-López et al., 2018). In addition, interaction type, strength, and
474 effect (positive or negative) is expected to vary with species ontogeny (development of organisms
475 within their lifespan), for example, herbivores turning into pollinators or alternating predation-
476 competition. Thus, including the broad scope of interactions within the lifespan of species would be
477 more accurate than focusing on seasonal ones (Yang & Rudolf, 2010). Despite some efforts to provide
478 frameworks for the study of phenology (Visser et al., 2010) and the shifts of phenology-ontogeny (Yang
479 & Rudolf, 2010), there is a need to define a common framework for research addressing biotic
480 interactions within phenology. Here we propose a framework for the inclusion of biotic interactions

481 within phenology (Fig. 3), apportioning this into two interconnected factions where research is aimed
482 towards 1) conceptualising biotic interactions and 2) modelling biotic interactions.

483 Conceptualising the biotic interactions within phenology depends on the data, type of interaction, and
484 spatiotemporal dimension of the research. As identified throughout this review, there has been a wide
485 range of data used, including Julian day of phenological events and the presence and/or abundance
486 of species at a given location. This data represents various inter- and intra-species interactions that
487 include information on facilitated, obligated, and trophic relationships. Finally, the temporal and
488 spatial dimensions of these data and interactions are imperative for the methodologies implemented,
489 as this determines whether research focuses on a particular moment of the life cycle of a species or
490 across an extended time period (Yang & Rudolf, 2010). All this information is fundamental for
491 specifying whether the biotic interaction is measured directly through field or experimental research
492 or indirectly through the use of biodiversity proxies or co-existence records.

493 The consideration of co-existence as a biotic interaction or as a proxy of a biotic interaction has
494 received a renewed discussion among ecologists recently (Dormann et al., 2018; Blanchet, Cazelles &
495 Gravel, 2020; Peterson, Soberón, Ramsey & Osorio-Olvera, 2020). In the recent review by Blanchet et
496 al. (2020), the authors emphasise that co-existence records are a poor proxy for biotic interactions,
497 providing a detailed discussion arguing that very extensive (and rarely available) datasets would be
498 needed to test this, but more importantly the biotic interaction must exert a greater signal before it
499 can be inferred within co-existence records. Building on this foundation and the research incorporated
500 in this review, we agree with the premise and propose that studies that use historical temporal
501 datasets of multiple individual species or spatial datasets of multiple species presence-absence must
502 be considered co-existence studies rather than biotic interactions. This is due in part to the fact that
503 these studies often have different data collection methods for taxa and seldom directly record
504 interactions in the field. When coupled with the limitations identified in the statistical models in
505 section 2 (e.g., Austin, 2007), any signal of biotic interaction must be treated with caution.

Modelling of biotic interaction or co-existence is dependent on the variable representation. We have identified three common categories of variable representation; a) activity length (e.g., Julian days or mismatch indices - Mayor et al., 2017), biodiversity parameters (e.g., presence-absence, abundance, functional traits, richness gradients) and c) interaction rates (e.g., herbivory rate, predation rates, etc.). We have also identified that research addressing biotic interactions within phenology often considers the importance of abiotic factors. Subsequently, there is often a need to select both, which includes the type of abiotic parameters relevant to the question at hand. Selection of abiotic parameters is well established in phenology, but it remains important to consider the representation of variables (e.g., mean, max, min) and the appropriate spatial and temporal resolution (van de Pol et al., 2016; Holloway et al., 2018; Simmonds, Cole & Sheldon 2019). From these variables, the modelling approaches identified through Sections 2-5 should then be selected according to the most appropriate data, interaction, spatiotemporal dimension, and biotic representation. Importantly, not all representations are suitable for all methods, highlighted in Fig 3. Such a framework should foster discussion among researchers investigating co-existence and biotic interactions within phenology research and provide signposts for researchers aiming to begin initial work in this discipline.

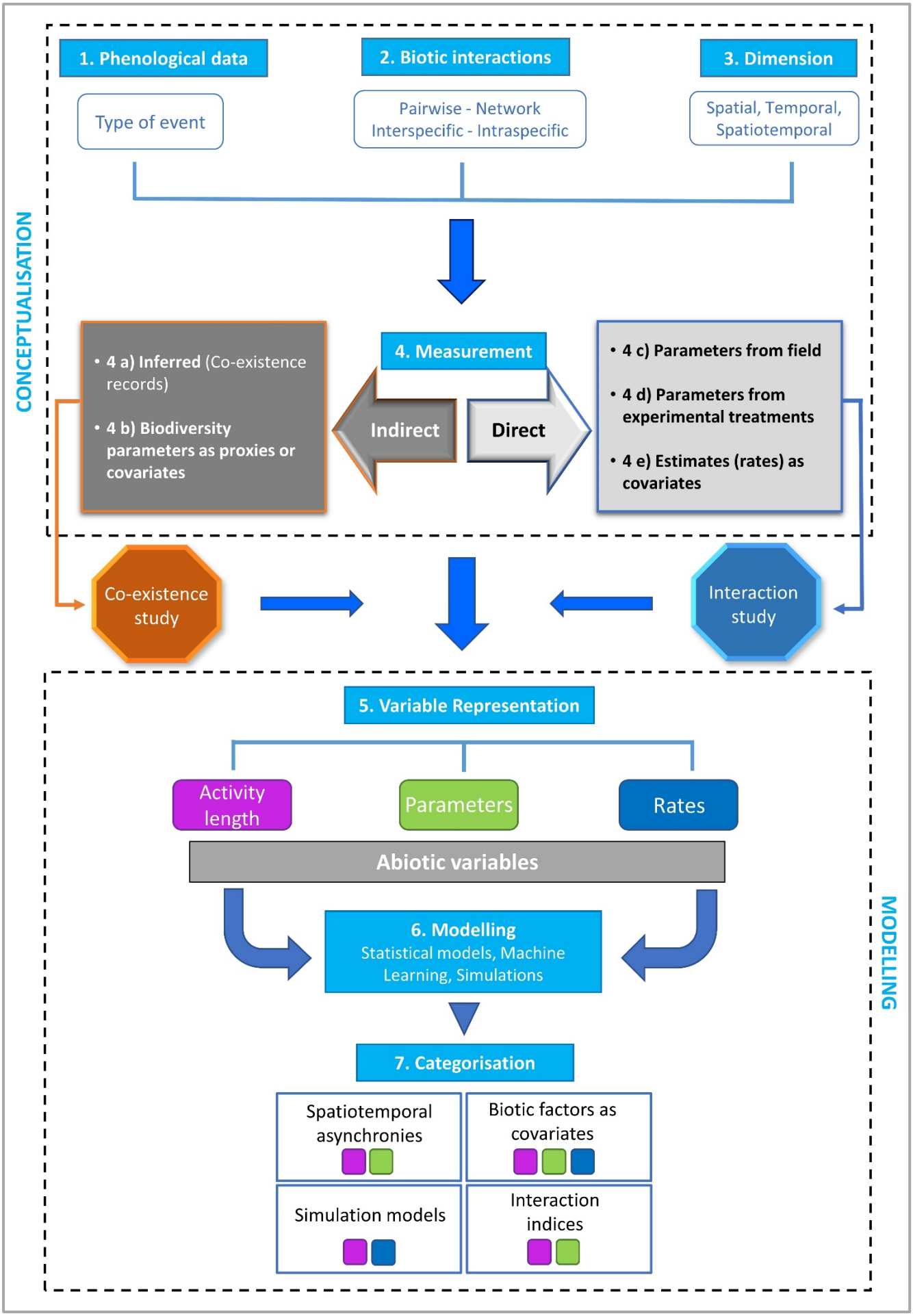

CONCEPTUALISATION
1. Phenological data
Type of event
2. Biotic interactions
Pairwise - Network
Interspecific - Intraspecific
3. Dimension
Spatial, Temporal,
Spatiotemporal
4. Measurement
Indirect
Direct
• 4 a) Inferred (Co-existence records)
• 4 b) Biodiversity parameters as proxies or covariates
• 4 c) Parameters from field
• 4 d) Parameters from experimental treatments
• 4 e) Estimates (rates) as covariates
Co-existence study
Interaction study
MODELLING
5. Variable Representation
Activity length
Parameters
Rates
Abiotic variables
6. Modelling
Statistical models, Machine Learning, Simulations
7. Categorisation
Spatiotemporal asynchronies
Biotic factors as covariates
Simulation models
Interaction indices

Figure 3. Framework illustrating the conceptualisation and modelling of biotic interactions in phenology research. Conceptualisation occurs during points 1 to 4, in which researchers need to identify the type of event (1), which refers to the phenological event of study, e.g. flowering time, emergence time, first flight, bud burst, etc., then the interactions of interest (2), e.g., pairwise or network, inter or intra-specific, and type of interaction i.e. trophic (herbivory, predation, etc.), positive (facilitation, mutualism, commensalism), negative (competence, amensalim) or neutral. Then researchers must consider the dimension (3) of study, which accounts for the different spatial and temporal extent of the variables that will shape the modelling process. Finally, this will lead to the measurement of biotic interactions (4), in which we discriminate between indirect (4a-b) and direct (4c-e) measurements. Indirect measurements include those that have been quantified from co-existence records (4a) or parameters that use proxies or covariates (4b), including presence-absence and functional traits. Direct measurements include parameters directly monitored in the field (4c), including pollinator visitation, parameters from experimental treatments (4d), including manipulated vs non-manipulated individuals, and estimates (rates) as covariates (4e), including predation or herbivory rates. We propose that indirect measurements should proceed as co-existence studies, while direct measures should proceed as interaction studies. The modelling of biotic interactions and co-existence studies occurs during points 5-7. There are three main ways in which the study variables are often represented (5): Activity length (purple box) i.e. differences in arrival date, emergence date, flowering time, typically measured in Julian or calendar days. Parameters (green box), when variables of study are ecological measurements such as richness, functional traits, distribution of interactors, presence - absence data, etc., and Rates (blue box), when the variables are estimated as a measurement of a biotic interaction, e.g. predation rate, parasitism rate, pollination success. The selected variables together with the abiotic variables of interest are then modelled (6) using the approaches applicable for the study of biotic interactions, leading to (7) the four identified categories where coloured quadrats (purple, blue and green) in the lower box symbolize the type of variable representation typically incorporated in the different modelling approaches.

7 Emerging Opportunities and Challenges

7.1 Spatial Modelling through SDM

Accounting for the complexity that phenological events pose at both spatial and temporal scales is difficult. With advances in data collection, SDMs (as described in section 2) are now being parameterised more readily with temporally explicit variables (e.g., normalized difference vegetation index (NDVI) for the date closest to the timestamped species observation). This removes some of the uncertainty in projecting seasonal distributions (Holloway & Miller, 2017), with the distribution projections being used as estimates for phenological events. For example, Gschweng, Kalko, Berthold, Fiedler, and Fahr (2012) matched telemetry data with meteorological and habitat data to project monthly distributions of the Eleonara's falcon in Madagascar, identifying seasonal patterns of distributions, and relating this to the timing of migration events. Distribution projections could

theoretically be generated at finer (e.g., daily, weekly, or monthly) timescales, which may capture important information regarding the relationship between phenological events and species distributions. Figure 4 provides an illustrative example of SDM projections for the migratory barn swallow within the island of Ireland parameterized on spatially and temporally explicit observations and environmental data. The increase in habitat suitability for barn swallows in April aligns with their migration, and supports the premise that SDMs parameterised on averaged climate variables (e.g., mean temperature) have often failed to capture the actual variability that species experience in short time periods which drive changes in the spatial distributions across the life cycle (Eyre, Rushton, Luff & Telfer, 2005).

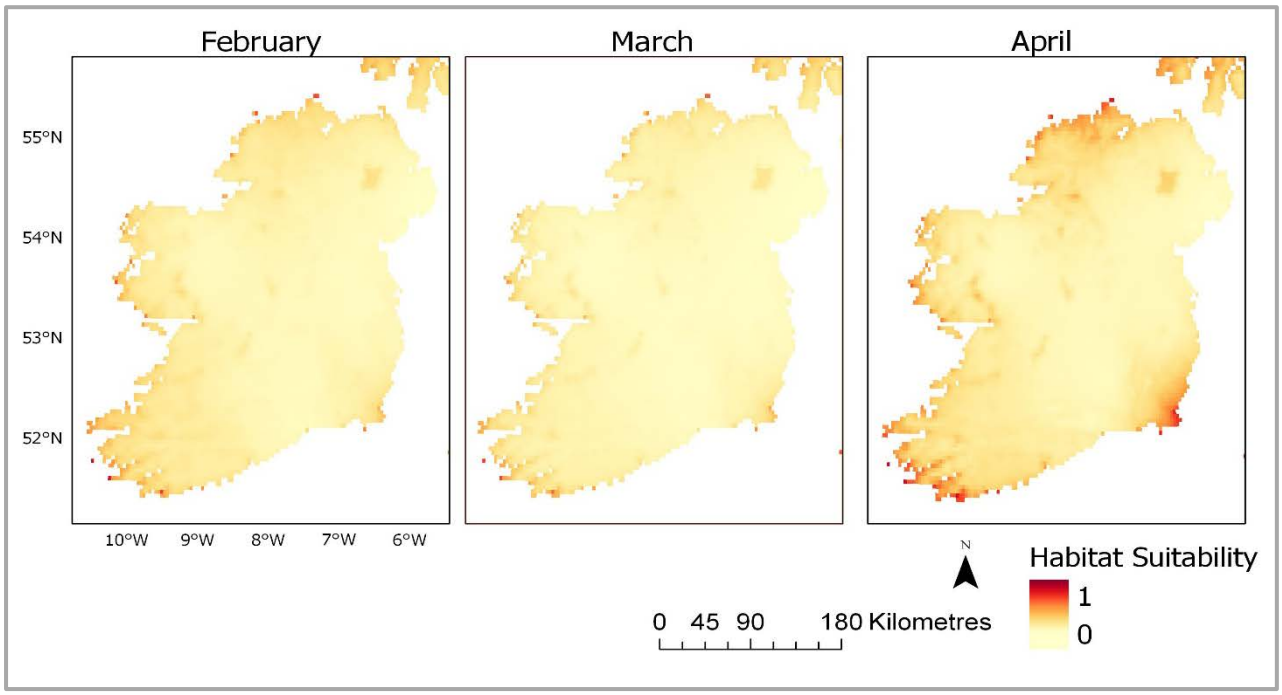


Figure 4. Example of monthly habitat suitabiltiy of a migrant bird, Barn Swallow, in Ireland, projected using temporally explicit temperature data and presence data using a generalised linear model (GLM). Barn swallow data extracted from 2018 presence records of eBird (2017) dataset (Sullivan et al., 2009), temperature data, monthly max and min values, extracted from Worldclim 2.0 database (Fick & Hijmans, 2017).

Several recent and thorough reviews within SDM explore the role of biotic interactions in model parameterisation using both correlative and joint-SDM (e.g., Wisz et al., 2013; Dormann et al., 2018;

Peterson et al., 2020), and as such it is not our aim to duplicate efforts. Instead, we highlight challenges and frontiers of incorporating biotic interactions within SDM and identify where phenological research could learn from this burgeoning field. The inclusion of biotic parameters (representing interactions or co-existence) in SDMs generally leads to improvement of predictive power of the models (Atauchi et al., 2017; Palacio & Girini, 2018), however, the fact that a model integrates biotic parameters does not always increase model accuracy (e.g., Holloway, 2018). In some cases when the considered biotic interactors are highly correlated to abiotic parameters, for example climatic conditions that determine presence of a particular species, the inclusion of biotic factors in model parameterisation might result in multicollinearity or show no improvements of SDMs due to the overarching influence of abiotic conditions (Silva et al., 2014). Recently, Raath, Le Roux, Veldtman and Greve (2018) compared four methods of incorporating biotic factors, by using different representations of host-plant distributions in SDMs of two silk moth species in sub-Saharan Africa. They found that inclusion of moth-host plant interactions in SDM greatly affected the predictive ability of the models, yet there was inconsistency among biotic representation. The inclusion of temporally explicit quantified biotic factors in SDM is rare (although note Mezquida, Svenning, Summers & Benkman (2018) who recorded the spatial timings of seed fall for European Scots pine and included this as a covariate in an SDM projecting the European distribution of crossbills), meaning studies have to rely on proxies for interactions within SDM. Thus, relevance of interactions and how interactions are represented in model parameterisation can shape the resulting outputs. With biotic representation a key component of our conceptual framework (Fig. 3), this subsequently warrants further research to investigate whether such patterns exist across multiple interactors and trophic levels within phenology.

7.2 Quantifying Interactions from New Technology

The use of new technology (e.g., acoustic recorders and telemetry data) has also been shown to provide novel insights for quantifying intra- and inter-species interactions (Isbell & Binder, 2016). Telemetry data acquires precise spatial and temporal animal position and movement data

(Hebblewhite & Haydon, 2010), having been used to capture information on phenological interactions, such as mating, boundary patrolling, and hunting (Long & Nelson 2013; Benhamou, Valeix, Chamaillé-Jammes, Macdonald & Loveridge, 2014 ; Long, Nelson, Weeb & Gee, 2014). Despite this advancement in technology, similar issues relating to the direct estimate of intra- and inter-species-specific interactions persists. For example, Miller (2012; 2015) tested several commonly implemented indices of dynamic interactions for brown hyenas in Botswana alongside a null model of movement. The results suggested that the use of 'expected' values in their generation produced inconsistent results, which led to both Type I and II errors in the model interpretation. The general consensus has been that such indices perform well at identifying no interaction between individuals; however, the majority of these models use proximity in space and time (i.e. co-existence) to infer interaction, meaning similar issues of interaction contextualisation persist. However, indirect interactions through smell or sight that impact movement behaviours (e.g., leading, following) are difficult to model due to the hierarchical nature of the processes, and may be considered as 'no interaction' in established indices due to the spatial and temporal asynchrony. New methods that consider the potential path area of movement trajectories in temporally asynchronous space are being developed that allow for such interactions to be quantified (Hoover, Miller & Long 2020).

Similarly, camera traps have also been used to capture information on phenology (e.g., Graham, Riordan, Yuen, Estrin & Rundel, 2010; Tape & Gustine 2014; Alberton et al., 2017), allowing the examination of community structures and interspecific interactions (Steinmetz, Seuaturien & Chutipong, 2013; Jachowski, Katzner, Rodrigue & Ford, 2015; Buxton et al., 2016; Camargo-Sanabria & Mendoza 2016). For example, Jachowski et al. (2015) used over 2.5 million images from over 180 camera traps to investigate interactions among raptor species (i.e. bald and golden eagle) in eastern continental USA in relation to their migration phenology and subsequent interactions. By analysing the presence of raptors in more than 2.5 million images, the authors found that bald and golden eagles were positively associated with each other, with the presence of golden eagles 55% more likely if a bald eagle was also sighted on the same day, suggesting a possible mutualistic interaction. The ability

of camera traps to capture observed interactions is a primary advantage to the technology. However, Koike et al. (2012) used camera traps to investigate herbivory by mammals of fruit produced by trees in Japan, and while the authors concluded that the animals visited the trees, the images did not necessarily confirm that the animals actually ate the fruit. Therefore, despite the potential of such technology, issues related to the quantification of the biotic interaction persist. Fig. 5 illustrates examples where camera traps, acoustic recorders, and telemetry data capture co-existence in space and time as well as direct interactions. New methods of quantifying these interactions, through image analysis, acoustic signals, and movement parameters will subsequently be needed to ascertain in what instances interactions can be recorded.

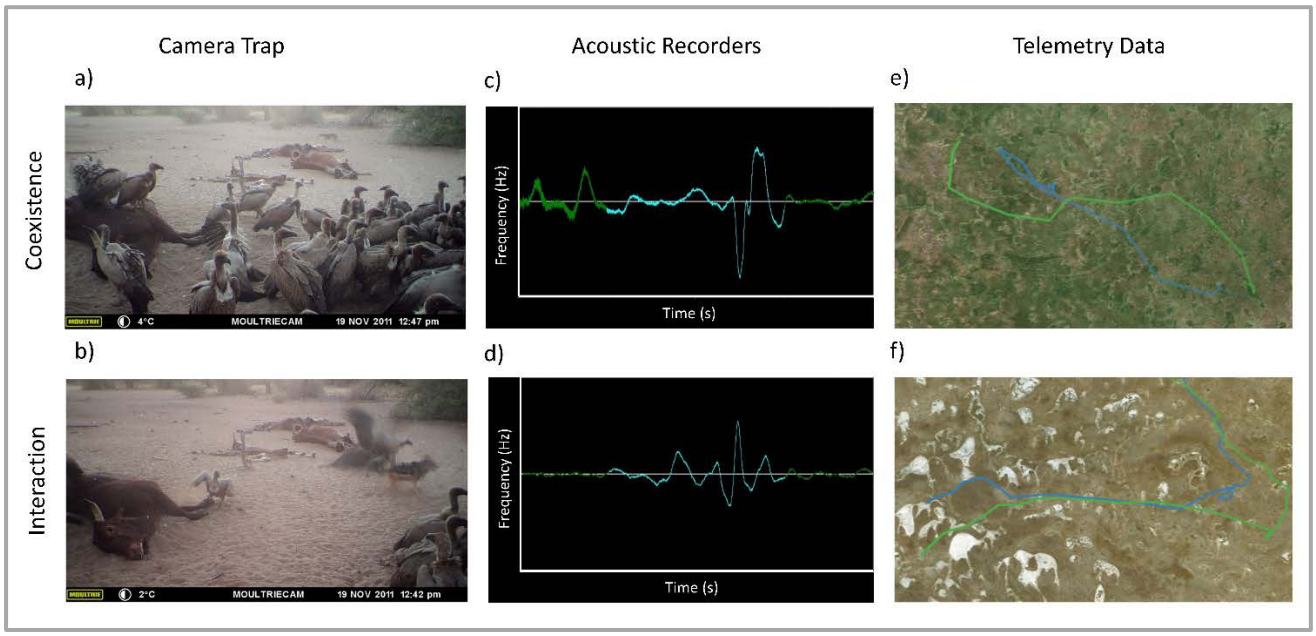


Figure 5. Illustration of co-existence between species versus biotic interactions using technology including camera traps, acoustic recorders, and telemetry data. Image captured from a camera traps in the Ghanzi region of Botswana, showing presence of black-back jackal and hooded vultures a) in the same location at same time, not interacting and b) an interaction (competition) between two individuals. Photo credit Thoralf Meyer. Audiograms from acoustic recorders (AudioMoth) (Hill et al., 2018) in Cork, Ireland, showing waveforms of recorded calls (green line), blue lines are the fragment of the calls analysed identifying vocalization, with SoundID (Boucher, 2014), c) illustrating co-existence, vocalizations of various individuals of two different *corvidae* species, jackdaw and rook, where no apparent interaction was taking place and d) illustrating interaction (competition) between jackdaws and rooks, with the audiogram reporting corresponding patterns for alarm and territorial calls. Global positioning system (GPS) of Burchill's zebra in Botswana, showing e) coexistence and f) interaction (herding) between individuals over a 24-hour period. Zebra data from Bartlam-Brooks et al. (2013a,b) via Movebank (2013), visualised in DYNAMO-Vis (Dodge, Xavier & Wong, 2018).

673 Remote sensing has also been widely used in phenology research, primarily to document phenological
674 events for vegetation, such as start-of-season or end-of-season (O'Connor, Dwyer, Cawkwell &
675 Eklundh, 2012; Barrett et al., 2014; Misra, Buras, Heurich, Asam & Menzel, 2018) or through the use
676 of active sensors (e.g., radar) to monitor animal migration events (e.g., Diehl, Larkin & Black 2003;
677 Schmaljohan, Liechti, Bächler, Steuri & Bruderer, 2008; Nilsson et al., 2018). These phenological
678 indicators (e.g., start-of-season, first-flight) are then used to identify spatial or temporal asynchronies
679 between interactor species or used as spatial representations of biotic factors in statistical models
680 (Morellato et al., 2016). UAV footage can be monitored to quantify interactions between individuals,
681 with Schofield, Katselidis, Lilley, Reina and Hays (2017) investigating whether departure of male turtles
682 from breeding sites was driven by changes in the receptiveness of females or the probability of
683 successful mating attempts, quantifying this through the sex ratio of all individuals within the footage.
684 Subsequently, drones offer a (relatively) non-invasive method to monitor phenological events of
685 inaccessible species. Remote sensing has also been used successfully to monitor species invasions
686 (Rocchini et al., 2015) through the reflectance properties of vegetation to classify different species to
687 identify competition among native and non-native species (e.g., Carter et al., 2009) and to identify
688 pest or disease emergence (e.g., He, Chen, Potter & Meentemeyer, 2019), with interactions inferred
689 through these indirect observations. Challenges associated with novel methods of classifying
690 hyperspectral images to delineate among plant species or identify pest-induced plant stress have been
691 identified as perhaps being more important than challenges associated with the resolution of such
692 data (Rocchini et al., 2015), which would allow for an improved species-level monitoring of
693 phenological events. However, the question of how to directly record inter-species interactions
694 through remote sensing remains, in part due to the relatively coarse-level data obtained from remote
695 sensing compared to the scale many biotic interactions occur at, suggesting a need for integration of
696 multiple technologies to address such challenges.

697 Integration of multiple technologies will provide new forms data on interactions among individuals,
698 populations, and species, which will then require novel methodologies for analysis. For example, Isbell

and Bidner (2016) used a combination of camera traps, acoustic recorders, and telemetry data to investigate the interactions between vervet monkeys and leopards in Kenya. Alarm calls recorded through the acoustic recorders revealed that these occurred most frequently at dusk and dawn, while camera traps revealed that leopards approached vervets most frequently at night when alarm-calls were initiated less. Telemetry data then identified the direction of movement of leopards associated with corresponding alarm calls from the acoustic devices, finding that when alarm calls were present, leopards moved quickly away up to 200m. Such a novel study identifies a successful framework for overcoming the individual limitations of each of the technologies, allowing interactions to be confirmed. However, the authors did not generate any quantification of these interactions, providing a qualitative description of the measurements. Such approaches could be extended to explore interactions directly related to phenological events, such as breeding success for prey species. Reviews are emerging that explore the utility of combining acoustic recorders with camera traps (Buxton et al., 2016), and technological advancements are combining GPS collars with remote cameras to provide context to interaction (Hebblewhite & Haydon 2010). The International Cooperation for Animal Research Using Space (ICARUS) has also recently launched, aiming to utilise satellite and tracking technology to observe the movement of small animals, providing a global approach to animal movement, which will undoubtedly provide new insights informing phenology and biotic interactions. Marion et al. (2020) provide an up-to-date review of methods for studying human-wildlife interactions using camera traps and telemetry data, with recommendations potentially applicable to studying biotic interactions in phenology research. It is evident that such interdisciplinary approaches are needed in this emerging research field.

8. Concluding remarks

Our review summarizes the current state of the art for methods employed for the evaluation of phenology and biotic interactions. We document a noticeable imbalance among both topics; phenology and biotic interactions, despite the important role biotic interactions have in phenological

processes, and vice versa. While studies investigating biotic interactions in phenology are relatively scarce, several studies across disparate disciplines have undertaken research, and can be broadly grouped into four main categories: 1) spatial and temporal asynchronies, 2) biotic factors as covariates, 3) simulation studies, and 4) interaction indices. Spatial and temporal mismatch studies have typically used historical datasets to infer changes in biotic interactions that are not measured from co-occurrence records (Gordo & Sanz, 2005) or SDM projected into future space and time to investigate changes in distributions among interactor species (Yun et al., 2020). Biotic factors as covariates studies have focused on trophic or obligated interactions since any change in one interactor is expected to have impact on the other (Post & Forchamer, 2007). However, experimental studies testing both abiotic and biotic factors are still rare (Alexander et al., 2015). Simulation studies of phenological events and biotic interactions are rare and have mainly been developed to test for changes in phenological events under different climatic scenarios (Bateman et al., 2016) or to evaluate changes in ecological networks by removing biotic components (Schleuning et al., 2016). Novel approaches developing interaction indices can help to develop new methodologies to document phenological events at broad regional scales (Buxton et al., 2016) as well as providing new insights for the monitoring of biotic interactions. Finally, we introduce a new framework that apportions biotic interactions into two interconnected factions where research is aimed towards 1) conceptualising biotic interactions within phenology and 2) modelling biotic interactions within phenology. Such a framework should provide researchers and practitioners with a basis to investigate interactions and co-existence successfully and robustly within the wider field of phenology.

8. Author contributions

RTC and PH conceptualised this review. RTC conducted the systematic portion of the review and wrote the first draft of the paper. PH provided inputs and helped in the editing process of the manuscript. Both authors were involved in the revision process.

9. Acknowledgements

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10. Data Availability

All data used to create figures are currently in open repositories. Data for figure 4 was extracted from ebird (2017) and WorldClim 2.0 database (Fick & Hijmans, 2017). Zebra data for figure 5 was from Bartlam-Brooks et al. (2013a, b) via Movebank (2013).

11. References

Alberton, B., Torres, R.D.S., Cancian, L.F., Borges, B.D., Almeida, J., Mariano, G.C., … Morellato, L.P.C., 2017. Introducing digital cameras to monitor plant phenology in the tropics: applications for conservation. Perspectives in Ecology and Conservation, 15(2), pp.82-90. doi:10.1016/j.pecon.2017.06.004

Alexander, J.M., Diez, J.M. and Levine, J.M., 2015. Novel competitors shape species' responses to climate change. Nature, 525(7570), pp.515-518. doi:10.1038/nature14952

Araújo, M.B., Rozenfeld, A., Rahbek, C. and Marquet, P.A., 2011. Using species co-occurrence networks to assess the impacts of climate change. Ecography, 34(6), pp.897-908. doi: 10.1111/j.1600-0587.2011.06919.x

Araújo, M.B. and Rozenfeld, A., 2014. The geographic scaling of biotic interactions. Ecography, *37*(5), pp.406-415. doi: 10.1111/j.1600-0587.2013.00643.x

773 Atauchi, P.J., Peterson, A.T. and Flanagan, J., 2018. Species distribution models for Peruvian
774 plantcutter improve with consideration of biotic interactions. Journal of Avian Biology, 49(3), pp.jav-
775 01617. doi:10.1111/jav.01617

776 Austin, M., 2007. Species distribution models and ecological theory: a critical assessment and some
777 possible new approaches. Ecological Modelling, 200(1-2), pp.1-19.
778 doi:10.1016/j.ecolmodel.2006.07.005

779 Bartlam-Brooks, H.L.A., Beck, P.S., Bohrer, G. and Harris, S., 2013a. In search of greener pastures –
780 using satellite images to predict the effects of environmental change on zebra migration. Journal of
781 Geophysical Research: Biogeosceinces, 188, 1–11. doi:10.1002/jgrg.20096

782 Bartlam-Brooks, H.L.A. and Harris, S., 2013b. Data from: in search of greener pastures: using satellite
783 images to predict the effects of environmental change on zebra migration. *Movebank Data Repository*.
784 doi:10.5441/001/1.f3550b4f

785 Barrett, B., Nitze, I., Green, S. and Cawkwell, F., 2014. Assessment of multi-temporal, multi-sensor
786 radar and ancillary spatial data for grasslands monitoring in Ireland using machine learning
787 approaches. Remote Sensing of Environment, 152, pp.109-124. doi: 10.1016/ j.rse.2014.05.018

788 Bartomeus, I., Ascher, J.S., Wagner, D., Danforth, B.N., Colla, S., Kornbluth, S. and Winfree, R., 2011.
789 Climate-associated phenological advances in bee pollinators and bee-pollinated plants. Proceedings
790 of the National Academy of Sciences, 108(51), pp.20645-20649. doi: 10.1073/pnas.1115559108/-
791 /DCSupplemental.

792 Bartomeus, I., Park, M.G., Gibbs, J., Danforth, B.N., Lakso, A.N. and Winfree, R., 2013. Biodiversity
793 ensures plant–pollinator phenological synchrony against climate change. Ecology Letters, 16(11),
794 pp.1331-1338. doi: 10.1111/ele.12170

795 Bascompte, J., Jordano, P. and Olesen, J. M., 2006. Asymmetric coevolutionary networks facilitate
796 biodiversity maintenance. Science, 312, pp.431-433. doi: 10.1126/science.1123412

797 Baselga, A. and Araújo, M.B., 2009. Individualistic vs community modelling of species distributions
798 under climate change. Ecography, 32(1), pp.55-65. doi: 10.1111/j.1600-0587.2009.05856.x

799 Bateman, B.L., VanDerWal, J., Williams, S.E. and Johnson, C.N., 2012. Biotic interactions influence the
800 projected distribution of a specialist mammal under climate change. Diversity and Distributions, 18(9),
801 pp.861-872. doi: 10.1111/j.1472-4642.2012.00922.x

802 Bateman, B.L., Pidgeon, A.M., Radeloff, V.C., VanDerWal, J., Thogmartin, W.E., Vavrus, S.J. and
803 Heglund, P.J., 2016. The pace of past climate change vs. potential bird distributions and land use in
804 the United States. Global Change Biology, 22(3), pp.1130-1144. doi: 10.1111/gcb.13154

805 Benadi, G., Hovestadt, T., Poethke, H.J. and Blüthgen, N., 2014. Specialization and phenological
806 synchrony of plant–pollinator interactions along an altitudinal gradient. Journal of Animal
807 Ecology, 83(3), pp.639-650. doi: 10.1111/1365-2656.12158

808 Benning, J.W., Eckhart, V.M., Geber, M.A. and Moeller, D.A., 2019. Biotic interactions contribute to
809 the geographic range limit of an annual plant: Herbivory and phenology mediate fitness beyond a
810 range margin. The American Naturalist, 193(6), pp.786-797. doi: 10.1086/703187

811 Benhamou, S., Valeix, M., Chamaillé-Jammes, S., Macdonald, D.W. and Loveridge, A.J., 2014.
812 Movement-based analysis of interactions in African lions. Animal Behaviour, 90, pp.171-180. doi:
813 10.1016/j.anbehav.2014.01.030

814 Blanchet, F.G., Cazelles, K. and Gravel, D., 2020. Co-occurrence is not evidence of ecological
815 interactions. Ecology Letters, 23, pp.1050–1063. doi: 10.1111/ele.13525

816 Blois, J.L., Zarnetske, P.L., Fitzpatrick, M.C. and Finnegan, S., 2013. Climate change and the past,
817 present, and future of biotic interactions. Science, 341(6145), pp.499-504. doi:
818 10.1126/science.1237184

819 Both, C., Van Asch, M., Bijlsma, R.G., Van Den Burg, A.B. and Visser, M.E., 2009. Climate change and
820 unequal phenological changes across four trophic levels: constraints or adaptations?. Journal of
821 Animal Ecology, 78(1), pp.73-83. doi: 10.1111/j.1365-2656.2008.01458.x

822 Boucher, N. J. 2014. SoundID version 2.0.0 documentation. – SoundID.

823 Bresson, J., Varoquaux, F., Bontpart, T., Touraine, B. and Vile, D., 2013. The PGPR strain
824 *Phyllobacterium brassicacearum* STM 196 induces a reproductive delay and physiological changes that
825 result in improved drought tolerance in *Arabidopsis*. New Phytologist, 200(2), pp.558-569. doi:
826 10.1111/nph.12383

827 Brzostek, E.R., Dragoni, D., Schmid, H.P., Rahman, A.F., Sims, D., Wayson, C.A., … Phillips, R.P., 2014.
828 Chronic water stress reduces tree growth and the carbon sink of deciduous hardwood forests. Global
829 Change Biology, 20(8), pp.2531-2539. doi: 10.1111/gcb.12528

830 Burkle, L.A., Marlin, J.C. and Knight, T.M., 2013. Plant-pollinator interactions over 120 years: loss of
831 species, co-occurrence, and function. Science, 339(6127), pp.1611-1615. doi:
832 10.1126/science.1232728

833 Buxton, R.T., Brown, E., Sharman, L., Gabriele, C.M. and McKenna, M.F., 2016. Using bioacoustics to
834 examine shifts in songbird phenology. Ecology and Evolution, 6(14), pp.4697-4710. doi:
835 10.1002/ece3.2242

836 Camargo-Sanabria, A.A. and Mendoza, E., 2016. Interactions between terrestrial mammals and the
837 fruits of two neotropical rainforest tree species. Acta Oecologica, 73, pp.45-52.
838 https://doi.org/10.1016/j.actao.2016.02.005

839 CaraDonna, P.J., Petry, W.K., Brennan, R.M., Cunningham, J.L., Bronstein, J.L., Waser, N.M. and
840 Sanders, N.J., 2017. Interaction rewiring and the rapid turnover of plant–pollinator networks. Ecology
841 Letters, 20(3), pp.385-394. doi: 10.1111/ele.12740

842 Chmura, H.E., Kharouba, H.M., Ashander, J., Ehlman, S.M., Rivest, E.B. and Yang, L.H., 2019. The
843 mechanisms of phenology: the patterns and processes of phenological shifts. Ecological Monographs,
844 89(1), p.e01337. doi: 10.1002/ecm.1337

845 Chuine, I. and Régnière, J., 2017. Process-based models of phenology for plants and animals. Annual
846 Review of Ecology, Evolution, and Systematics, 48, pp.159-182. doi: 10.1146/annurev-ecolsys-110316-
847 022706

848 Deichmann, J.L., Acevedo-Charry, O., Barclay, L., Burivalova, Z., Campos-Cerqueira, M., d'Horta, F., …
849 Linke, S., 2018. It's time to listen: there is much to be learned from the sounds of tropical ecosystems.
850 Biotropica, 50(5), pp.713-718. doi: 10.1111/btp.12593

851 Diehl, R.H., Larkin, R.P. and Black, J.E., 2003. Radar observations of bird migration over the Great
852 Lakes. The Auk, 120(2), pp.278-290. doi: 10.1093/auk/120.2.278

853 Dixon, A.F.G., Glen, D.M., 1971. Morph determination in the bird-cherry oat aphid*, Rhopalosiphum*
854 *padi* (L). Ann. Appl. Biol. 68, pp.11–21. doi: 10.1111/j.1744-7348.1971.tb04633.x

855 Dodge, S., Xavier, G., and Wong, W.Y., 2018. DynamoVis - Dynamic Visualization of Animal Movement
856 Data. Retrieved from the *Data Repository for the University of Minnesota*. doi: 10.13020/D6PH49.

857 Donoso, I., Stefanescu, C., Martínez-Abraín, A. and Traveset, A., 2016. Phenological asynchrony in
858 plant–butterfly interactions associated with climate: a community-wide perspective. Oikos, 125(10),
859 pp.1434-1444. doi: 10.1111/oik.03053

860 Dormann, C.F., Bobrowski, M., Dehling, D.M., Harris, D.J., Hartig, F., Lischke, H., … Schmidt, S.I., 2018.
861 Biotic interactions in species distribution modelling: 10 questions to guide interpretation and avoid
862 false conclusions. Global Ecology and Biogeography, 27(9), pp.1004-1016. doi: 10.1111/geb.12759

863 Duchenne, F., Thébault, E., Michez, D., Elias, M., Drake, M., Persson, … Fontaine, C., 2020. Phenological
864 shifts alter the seasonal structure of pollinator assemblages in Europe. Nature Ecology &
865 Evolution, 4(1), pp.115-121. doi: 10.1038/s41559-019-1062-4f

866 Dullinger, S., Gattringer, A., Thuiller, W., Moser, D., Zimmermann, N.E., Guisan, A., … Caccianiga, M.,
867 2012. Extinction debt of high-mountain plants under twenty-first-century climate change. Nature
868 Climate Change, 2(8), pp.619-622. doi: 10.1038/NCLIMATE1514

869 Dunn, P.O. and Møller, A.P., 2014. Changes in breeding phenology and population size of birds. Journal
870 of Animal Ecology, 83(3), pp.729-739. doi: 10.1111/1365-2656.12162

871 eBird. 2017. eBird: An online database of bird distribution and abundance [web application]. eBird,
872 Cornell Lab of Ornithology, Ithaca, New York. Available: http://www.ebird.org. (Accessed: January 30,
873 2020).

874 Elith, J. and Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction
875 across space and time. Annual review of Ecology, Evolution, and Systematics, 40, pp.677-697.
876 https://doi.org/10.1146/annurev.ecolsys.110308.120159

877 Eyre, M.D., Rushton, S.P., Luff, M.L. and Telfer, M.G., 2005. Investigating the relationships between
878 the distribution of British ground beetle species (Coleoptera, Carabidae) and temperature,
879 precipitation and altitude. Journal of Biogeography, 32(6), pp.973-983. doi:10.1111/j.1365-
880 2699.2005.01258.x

881 Fick, S. E. and Hijmans, R. J. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global
882 land areas. – Int. J. Climatol. 4315: 4302–4315. doi: 10.1002/joc.5086

883 Forrest, J. and Miller-Rushing, A.J., 2010. Toward a synthetic understanding of the role of phenology
884 in ecology and evolution, 365, pp.3101–3112. doi:10.1098/rstb.2010.0145

885 Gallinat, A.S., Primack, R.B. and Wagner, D.L., 2015. Autumn, the neglected season in climate change
886 research. Trends in Ecology & Evolution, 30(3), pp.169-176. doi:10.1016/j.tree.2015.01.004

887 Goberville, E., Hautekèete, N.C., Kirby, R.R., Piquot, Y., Luczak, C. and Beaugrand, G., 2016. Climate
888 change and the ash dieback crisis. Scientific Reports, 6(1), pp.1-9. doi: 10.1038/srep35303

889 Gordo, O. and Sanz, J.J., 2005. Phenology and climate change: a long-term study in a Mediterranean
890 locality. Oecologia, 146(3), pp.484-495. doi: 10.1007/s00442-005-0240-z

891 Gordo, O. and Sanz, J.J., 2006. Climate change and bird phenology: a long-term study in the Iberian
892 Peninsula. Global Change Biology, 12(10), pp.1993-2004. doi: 10.1111/j.1365-2486.2006.01178.x

893 Graham, E.A., Riordan, E.C., Yuen, E.M., Estrin, D. and Rundel, P.W., 2010. Public Internet-connected
894 cameras used as a cross-continental ground-based plant phenology monitoring system. Global Change
895 Biology, 16(11), pp.3014-3023. doi: 10.1111/j.1365-2486.2010.02164.x

896 Graham, C.H. and Weinstein, B.G., 2018. Towards a predictive model of species interaction beta
897 diversity. Ecology Letters, 21(9), pp.1299-1310. doi: 10.1111/ele.13084

898 Gschweng, M., Kalko, E.K., Berthold, P., Fiedler, W. and Fahr, J., 2012. Multi-temporal distribution
899 modelling with satellite tracking data: predicting responses of a long-distance migrant to changing
900 environmental conditions. Journal of Applied Ecology, 49(4), pp.803-813. doi:0.1111/j.1365-
901 2664.2012.02170.x

902 He, Y., Chen, G., Potter, C. and Meentemeyer, R.K., 2019. Integrating multi-sensor remote sensing and
903 species distribution modelling to map the spread of emerging forest disease and tree
904 mortality. Remote sensing of Environment, 231, p.111238. doi: 10.1016/j.rse.2019.111238

905 Hebblewhite, M. and Haydon, D.T., 2010. Distinguishing technology from biology: a critical review of
906 the use of GPS telemetry data in ecology. Philosophical Transactions of the Royal Society B: Biological
907 Sciences, 365(1550), pp.2303-2312. doi:10.1098/rstb.2010.0087

908 Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.L. and Totland, Ø., 2009. How does climate warming
909 affect plant-pollinator interactions?. Ecology Letters, 12(2), pp.184-195. doi: 10.1111/j.1461-
910 0248.2008.01269.x

911 Hill, A. P., Prince, P., Piña-Covarrubias, E., Doncaster, C.P., Snaddon, J. L. and Rogers, A. AudioMoth:
912 Evaluation of a smart open acoustic device for monitoring biodiversity and the environment. Methods
913 in Ecology and Evolution, 9 (5), pp. 1199-1211. doi: 10.1111/2041-210X.12955

914 Holloway, P. 2018. Simulating movement-related resource dynamics to improve species distribution
915 models: A case study with oilbirds in northern South America. The Professional Geographer 70(4), 528-
916 540. doi:10.1080/00330124.2018.1479972

917 Holloway, P., Kudenko, D. and Bell, J.R., 2018. Dynamic selection of environmental variables to
918 improve the prediction of aphid phenology: A machine learning approach. Ecological Indicators, 88,
919 pp.512-521. doi: 10.1016/j.ecolind.2017.10.032

920 Holloway, P, and Miller, J.A. 2017. A quantitative synthesis of the movement concepts used within
921 species distribution modelling. Ecological Modelling, 356,pp.91-103.
922 doi: 10.1016/j.ecolmodel.2017.04.005
923 Hoover, B.A., Miller, J.A. and Long, J., 2020. Mapping areas of asynchronous-temporal interaction in
924 animal-telemetry data. Transactions in GIS, 24, pp.573–586. doi: 10.1111/tgis.12622

925 IPCC, 2018: Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C
926 above pre-industrial levels and related global greenhouse gas emission pathways, in the context of
927 strengthening the global response to the threat of climate change, sustainable development, and
928 efforts to eradicate poverty [Masson-Delmotte, V., Zhai, P., Pörtner, H.-O., Roberts, D., Skea, J., Shukla,
929 P.R., … Waterfield, T. (eds.)]. World Meteorological Organization, Geneva, Switzerland, 32 pp.

930 Isbell, L.A. and Bidner, L.R., 2016. Vervet monkey (Chlorocebus pygerythrus) alarm calls to leopards
931 (*Panthera pardus*) function as a predator deterrent. Behaviour, 153(5), pp.591-606. doi: 568539X-
932 00003365

933 Jachowski, D.S., Katzner, T., Rodrigue, J.L. and Ford, W.M., 2015. Monitoring landscape-level
934 distribution and migration Phenology of Raptors using a volunteer camera-trap network. Wildlife
935 Society Bulletin, 39(3), pp.553-563. doi:10.1002/wsb.571

936 Jones, T. and Cresswell, W., 2010. The phenology mismatch hypothesis: are declines of migrant birds
937 linked to uneven global climate change?. Journal of Animal Ecology, 79(1), pp.98-108. doi:
938 10.1111/j.1365-2656.2009.01610.x

939 Junker, R.R., Blüthgen, N., Brehm, T., Binkenstein, J., Paulus, J., Martin Schaefer, H. and Stang, M.,
940 2013. Specialization on traits as basis for the niche-breadth of flower visitors and as structuring
941 mechanism of ecological networks. Functional Ecology, 27(2), pp.329-341. doi: 10.1111/1365-
942 2435.12005

943 Kass, J.M., Anderson, R.P., Espinosa-Lucas, A., Juárez-Jaimes, V., Martínez-Salas, E., Botello, F., …
944 Sánchez-Cordero, V., 2020. Biotic predictors with phenological information improve range estimates
945 for migrating monarch butterflies in Mexico. Ecography, 43(3), pp.341-352. doi: 10.1111/ecog.04886

946 Keenan, T.F., Gray, J., Friedl, M.A., Toomey, M., Bohrer, G., Hollinger, D.Y., … Yang, B., 2014. Net carbon
947 uptake has increased through warming-induced changes in temperate forest phenology. Nature
948 Climate Change, 4(7), pp.598-604. doi: 10.1038/NCLIMATE2253

949 Keith, D.A., Akçakaya, H.R., Thuiller, W., Midgley, G.F., Pearson, R.G., Phillips, S.J., … Rebelo, T.G., 2008.
950 Predicting extinction risks under climate change: coupling stochastic population models with dynamic
951 bioclimatic habitat models. Biology Letters, 4(5), pp.560-563. doi: 10.1098/rsbl.2008.0049

952 Kharouba, H.M., Ehrlén, J., Gelman, A., Bolmgren, K., Allen, J.M., Travers, S.E. and Wolkovich, E.M.,
953 2018. Global shifts in the phenological synchrony of species interactions over recent decades.
954 Proceedings of the National Academy of Sciences, 115(20), pp.5211-5216. doi:10.1073/
955 pnas.1714511115

Koike, S., Kozakai, C., Morimoto, H., Arimoto, I., Yamazaki, K., Kasai, S. and Goto, Y., 2012. Relationships between the fruiting phenology of *Prunus jamasakura* and timing of visits by mammals-estimation of the feeding period using camera traps. In *Phenology and Climate Chagne.* INTECH Open Access Publisher. doi: 10.5772/35732

Koyama, A. and Tsuyuzaki, S., 2013. Facilitation by tussock-forming species on seedling establishment collapses in an extreme drought year in a post-mined *Sphagnum* peatland. Journal of Vegetation Science, 24(3), pp.473-483. doi: 10.1111/j.1654-1103.2012.01474.x

Lau, J.A. and Lennon, J.T., 2012. Rapid responses of soil microorganisms improve plant fitness in novel environments. Proceedings of the National Academy of Sciences, 109(35), pp.14058-14062. doi: 10.1073/pnas.1202319109/-/DCSupplemental.

Le Quéré, C., Andrew, R.M., Friedlingstein, P., Sitch, S., Hauck, J., Pongratz, J., … Arneth, A., 2018. Global carbon budget 2018. Earth System Science Data, 10(4), pp.2141-2194. doi: doi.org/10.5194/essd-10-2141

Long, J.A. and Nelson, T.A., 2013. Measuring dynamic interaction in movement data. Transactions in GIS, 17(1), pp.62-77. doi:10.1111/j.1467-9671.2012.01353.x

Long, J.A., Nelson, T.A., Webb, S.L. and Gee, K.L., 2014. A critical examination of indices of dynamic interaction for wildlife telemetry studies. Journal of Animal Ecology, 83(5), pp.1216-1233. doi: 10.1111/1365-2656.12198

Lu, X., Siemann, E., Shao, X., Wei, H. and Ding, J., 2013. Climate warming affects biological invasions by shifting interactions of plants and herbivores. Global Change Biology, 19(8), pp.2339-2347. doi: 10.1111/gcb.12244

Makoto, K., Kajimoto, T., Koyama, L., Kudo, G., Shibata, H., Yanai, Y. and Cornelissen, J.H.C., 2014. Winter climate change in plant–soil systems: summary of recent findings and future perspectives. Ecological Research, 29(4), pp.593-606. doi: 10.1007/s11284-013-1115-0

Marion, S., Davies, A., Demšar, U., Irvine, R.J., Stephens, P.A. and Long, J., 2020. A systematic review of methods for studying the impacts of outdoor recreation on terrestrial wildlife. Global Ecology and Conservation, p.e00917. doi: 10.1016/j.gecco.2020.e00917

Martin, T.E. and Maron, J.L., 2012. Climate impacts on bird and plant communities from altered animal–plant interactions. Nature Climate Change, 2(3), pp.195-200. doi: 10.1038/NCLIMATE1348

Mayor, S.J., Guralnick, R.P., Tingley, M.W., Otegui, J., Withey, J.C., Elmendorf, S.C., … Schneider, D.C., 2017. Increasing phenological asynchrony between spring green-up and arrival of migratory birds. Scientific Reports, 7(1), pp.1-10. doi:10.1038/s41598-017-02045-z

Memmott, J., Waser, N.M. and Price, M.V., 2004. Tolerance of pollination networks to species extinctions. Proceedings of the Royal Society of London. Series B: Biological Sciences, 271(1557), pp.2605-2611. doi:10.1098/rspb.2004.2909

Memmott, J., Craze, P.G., Waser, N.M. and Price, M.V., 2007. Global warming and the disruption of plant–pollinator interactions. Ecology Letters, 10(8), pp.710-717. doi:10.1111/j.1461-0248.2007.01061.x

Merrill, R.M., Gutiérrez, D., Lewis, O.T., Gutiérrez, J., Díez, S.B. and Wilson, R.J., 2008. Combined effects of climate and biotic interactions on the elevational range of a phytophagous insect. Journal of Animal Ecology, 77(1), pp.145-155. doi: 10.1111/j.1365-2656.2007.01303.x

Mezquida, E.T., Svenning, J.C., Summers, R.W. and Benkman, C.W., 2018. Higher spring temperatures increase food scarcity and limit the current and future distributions of crossbills. Diversity and Distributions, 24(4), pp.473-484. DOI: 10.1111/ddi.12694

Miller, J.A., 2012. Using spatially explicit simulated data to analyze animal interactions: a case study with brown hyenas in northern Botswana. Transactions in GIS, 16(3), pp.271-291. doi: 10.1111/j.1467-9671.2012.01323.x

1003 Miller, J.A., 2015. Towards a better understanding of dynamic interaction metrics for wildlife: a null
1004 model approach. Transactions in GIS, 19(3), pp.342-361. doi:10.1111/j.1467-9671.2012.01323.x

1005 Misra, G., Buras, A., Heurich, M., Asam, S. and Menzel, A., 2018. LiDAR derived topography and forest
1006 stand characteristics largely explain the spatial variability observed in MODIS land surface
1007 phenology. Remote Sensing of Environment, 218, pp.231-244. doi: 10.1016/ j.rse.2018.09.027

1008 Mohandass, D., Campbell, M.J., Chen, X.S. and Li, Q.J., 2018. Flowering and fruiting phenology of
1009 woody trees in the tropical-seasonal rainforest, Southwestern China. Current Science, 114(11),
1010 pp.2313-2322. doi: 10.18520/cs/v114/i11/2313-2322

1011 Molina-Venegas, R., Aparicio, A., Lavergne, S. and Arroyo, J., 2016. How soil and elevation shape local
1012 plant biodiversity in a Mediterranean hotspot. Biodiversity and Conservation, 25(6), pp.1133-1149.
1013 doi: 10.1007/s10531-016-1113-y

1014 Morellato, L.P.C., Alberton, B., Alvarado, S.T., Borges, B., Buisson, E., Camargo, , … Peres, C.A., 2016.
1015 Linking plant phenology to conservation biology. Biological Conservation, 195, pp.60-72. doi:
1016 10.1016/j.biocon.2015.12.033

1017 Morente-López, J., Lara-Romero, C., Ornosa, C. and Iriondo, J.M., 2018. Phenology drives species
1018 interactions and modularity in a plant-flower visitor network. Scientific Reports, 8(1), pp.1-11. doi:
1019 10.1038/s41598-018-27725-2

1020 Nilsson, C., Dokter, A.M., Schmid, B., Scacco, M., Verlinden, L., Bäckman, J., … Liechti, F., 2018. Field
1021 validation of radar systems for monitoring bird migration. Journal of Applied Ecology, 55(6), pp.2552-
1022 2564. doi: 10.1111/1365-2664.13174

1023 Oleques, S.S., Overbeck, G.E. and de Avia Jr, R.S., 2017. Flowering phenology and plant-pollinator
1024 interactions in a grassland community of Southern Brazil. Flora, 229, pp.141-146. doi:
1025 10.1016/j.flora.2017.02.024

1026 Olito, C. and Fox, J.W., 2015. Species traits and abundances predict metrics of plant–pollinator
1027 network structure, but not pairwise interactions. Oikos, 124(4), pp.428-436. doi: 10.1111/oik.01439

1028 Oliver, T.H., Heard, M.S., Isaac, N.J., Roy, D.B., Procter, D., Eigenbrod, F., … Proença, V., 2015.
1029 Biodiversity and resilience of ecosystem functions. Trends in Ecology & Evolution, 30(11), pp.673-684.
1030 doi: 10.1016/j.tree.2015.08.009

1031 Oliver, R.Y., Ellis, D.P., Chmura, H.E., Krause, J.S., Pérez, J.H., Sweet, S.K, … Boelman, N.T., 2018.
1032 Eavesdropping on the Arctic: Automated bioacoustics reveal dynamics in songbird breeding
1033 phenology. Science Advances, 4(6), p.eaaq1084. doi: 10.1126/sciadv.aaq1084

1034 O'Connor, B., Dwyer, E., Cawkwell, F. and Eklundh, L., 2012. Spatio-temporal patterns in vegetation
1035 start of season across the island of Ireland using the MERIS Global Vegetation Index. ISPRS Journal of
1036 Photogrammetry and Remote Sensing, 68, pp.79-94. doi: 10.1016/j.isprsjprs.2012.01.004

1037 O'Neill, B.F., Bond, K., Tyner, A., Sheppard, R., Bryant, T., Chapman, J., … Donnelly, A., 2012. Climatic
1038 change is advancing the phenology of moth species in Ireland. Entomologia Experimentalis et
1039 Applicata, 143(1), pp.74-88. doi: 10.1111/j.1570-7458.2012.01234.x

1040 Palacio, F.X. and Girini, J.M., 2018. Biotic interactions in species distribution models enhance model
1041 performance and shed light on natural history of rare birds: a case study using the straight-billed
1042 reedhaunter *Limnoctites rectirostris*. Journal of Avian Biology, 49(11), p.e01743. doi:
1043 10.1111/jav.01743

1044 Pau, S., Wolkovich, E.M., Cook, B.I., Davies, T.J., Kraft, N.J., Bolmgren, K., … Cleland, E.E., 2011.
1045 Predicting phenology by integrating ecology, evolution and climate science. Global Change Biology 17,
1046 pp.3633-3643. doi: 10.1111/j.1365-2486.2011.02515.x

1047 Peñuelas, J. and Filella, I., 2001. Responses to a warming world. Science, 294(5543), pp.793-795. doi:
1048 10.1126/science.1066860

1049 Peñuelas, J., T. Rutishauser, and I. Filella (2009), Phenology feedbacks on climate change, Science,
1050 324(5929), pp.887–888. doi:10.1126/science.1173004

1051 Peterson, A., Soberón, J., Pearson, J.R.G., Anderson, R. P., Martinez-Meyer, E., Nakamura, M. and
1052 Araújo, M. B. 2011. Ecological niches and geographic distributions (MPB-49). Princeton, NJ: Princeton
1053 University Press.

1054 Peterson, A.T., Soberón, J., Ramsey, J. and Osorio-Olvera, L., 2020. Co-occurrence networks do not
1055 support identification of biotic interactions. Biodiversity Informatics, 15(1), pp.1-10. doi:
1056 10.17161/bi.v15i1.9798

1057 Phillimore, A.B., Leech, D.I., Pearce-Higgins, J.W. and Hadfield, J.D., 2016. Passerines may be
1058 sufficiently plastic to track temperature-mediated shifts in optimum lay date. Global Change Biology,
1059 22(10), pp.3259-3272. doi: 10.1111/gcb.13302

1060 Pieretti, N., Farina, A. and Morri, D., 2011. A new methodology to infer the singing activity of an avian
1061 community: The Acoustic Complexity Index (ACI). Ecological Indicators, 11(3), pp.868-873. doi:
1062 10.1016/j.ecolind.2010.11.005

1063 Ponti, L., Cossu, Q.A. and Gutierrez, A.P., 2009. Climate warming effects on the *Olea europaea*–
1064 *Bactrocera oleae* system in Mediterranean islands: Sardinia as an example. Global Change Biology,
1065 15(12), pp.2874-2884. doi: 10.1111/j.1365-2486.2009.01938.

1066 Ponti, L., Gutierrez, A.P., Basso, B., Neteler, M., Ruti, P.M., Dell'Aquila, A. and Iannetta, M., 2013. Olive
1067 agroecosystems in the Mediterranean Basin: multitrophic analysis of climate effects with process-
1068 based representation of soil water balance. Procedia Environmental Sciences, 19, pp.122-131. doi:
1069 10.1016/j.proenv.2013.06.014

1070 Porfirio, L.L., Harris, R.M., Stojanovic, D., Webb, M.H. and Mackey, B., 2016. Projected direct and
1071 indirect effects of climate change on the Swift Parrot, an endangered migratory species. Emu-Austral
1072 Ornithology, 116(3), pp.273-283. doi: 10.1071/MU15094

1073 Post, E. and Forchhammer, M.C., 2008. Climate change reduces reproductive success of an Arctic
1074 herbivore through trophic mismatch. Philosophical Transactions of the Royal Society B: Biological
1075 Sciences, 363(1501), pp.2367-2373. doi:10.1098/rstb.2007.2207

1076 Primack, R.B., Higuchi, H. and Miller-Rushing, A.J., 2009. The impact of climate change on cherry trees
1077 and other species in Japan. Biological Conservation, 142(9), pp.1943-1949. doi:10.1016/
1078 j.biocon.2009.03.016

1079 Raath, M.J., Le Roux, P.C., Veldtman, R. and Greve, M., 2018. Incorporating biotic interactions in the
1080 distribution models of African wild silk moths (*Gonometa* species, Lasiocampidae) using different
1081 representations of modelled host tree distributions. Austral Ecology, 43(3), pp.316-327.
1082 doi:10.1111/aec.12569

1083 Rafferty, N.E. and Ives, A.R., 2011. Effects of experimental shifts in flowering phenology on plant–
1084 pollinator interactions. Ecology Letters, 14(1), pp.69-74. doi: 10.1111/j.1461-0248.2010.01557.x

1085 Richardson, A.D., Hollinger, D.Y., Dail, D.B., Lee, J.T., Munger, J.W. and O'keefe, J., 2009. Influence of
1086 spring phenology on seasonal and annual carbon balance in two contrasting New England forests. Tree
1087 Physiology, 29(3), pp.321-331. doi:10.1093/treephys/tpn040

1088 Roberts, A.M., Tansey, C., Smithers, R.J. and Phillimore, A.B., 2015. Predicting a change in the order of
1089 spring phenology in temperate forests. Global Change Biology, 21(7), pp.2603-2611. doi:
1090 10.1111/gcb.12896

1091 Robinson, S.V., Losapio, G. and Henry, G.H., 2018. Flower-power: Flower diversity is a stronger
1092 predictor of network structure than insect diversity in an Arctic plant–pollinator network. Ecological
1093 complexity, 36, pp.1-6. doi: 10.1016/j.ecocom.2018.04.005

1094 Rocchini, D., Andreo, V., Förster, M., Garzon-Lopez, C.X., Gutierrez, A.P., Gillespie, T.W., Hauffe, H.C.,
1095 He, K.S., Kleinschmit, B., Mairota, P. and Marcantonio, M., 2015. Potential of remote sensing to predict

species invasions: A modelling perspective. Progress in Physical Geography, 39(3), pp.283-309. doi: 10.1177/0309133315574659

Saino, N., Rubolini, D., Lehikoinen, E., Sokolov, L.V., Bonisoli-Alquati, A., Ambrosini, R., … Møller, A.P., 2009. Climate change effects on migration phenology may mismatch brood parasitic cuckoos and their hosts. Biology Letters, 5(4), pp.539-541. doi:10.1098/rsbl.2009.0312

Sargent, R.D. and Ackerly, D.D., 2008. Plant–pollinator interactions and the assembly of plant communities. Trends in Ecology & Evolution, 23(3), pp.123-130. doi:10.1098/rstb.2010.0145

Sayer, E.J., 2018. The anatomy of an excellent review paper. Functional Ecology, 32(10), pp.2278-2281. doi: 10.1111/1365-2435.13207

Schleuning, M., Fruend, J., Schweiger, O., Welk, E., Albrecht, J., Albrecht, M., … Boehning-Gaese, K., 2016. Ecological networks are more sensitive to plant than to animal extinction under climate change. Nature Communications, 7(1), pp.1-9. doi: 10.1038/ncomms13965

Schmaljohann, H., Liechti, F., Bächler, E., Steuri, T. and Bruderer, B., 2008. Quantification of bird migration by radar–a detection probability problem. Ibis, 150(2), pp.342-355.

Schofield, G., Katselidis, K.A., Lilley, M.K., Reina, R.D. and Hays, G.C., 2017. Detecting elusive aspects of wildlife ecology using drones: new insights on the mating dynamics and operational sex ratios of sea turtles. Functional Ecology, 31(12), pp.2310-2319. doi: 10.1111/1365-2435.12930

Schweiger, O., Biesmeijer, J.C., Bommarco, R., Hickler, T., Hulme, P.E., Klotz, S., … Petanidou, T., 2010. Multiple stressors on biotic interactions: how climate change and alien species interact to affect pollination. Biological Reviews, 85(4), pp.777-795. doi: 10.1111/j.1469-185X.2010.00125.x

Shonfield, J. and Bayne, E., 2017. Autonomous recording units in avian ecological research: current use and future applications. Avian Conservation and Ecology, 12(1). doi: 10.5751/ACE-00974-120114

1118 Silva, D.P., Gonzalez, V.H., Melo, G.A., Lucia, M., Alvarez, L.J. and De Marco Jr, P., 2014. Seeking the
1119 flowers for the bees: integrating biotic interactions into niche models to assess the distribution of the
1120 exotic bee species *Lithurgus huberi* in South America. Ecological Modelling, 273, pp.200-209. doi:
1121 10.1016/j.ecolmodel.2013.11.016

1122 Simmonds, E.G., Cole, E.F. and Sheldon, B.C., 2019. Cue identification in phenology: A case study of
1123 the predictive performance of current statistical tools. Journal of Animal Ecology, 88(9), pp.1428-1440.
1124 doi: 10.1111/1365-2656.13038

1125 de Souza Laurindo, R., Gregorin, R. and Tavares, D.C., 2017. Effects of biotic and abiotic factors on the
1126 temporal dynamic of bat-fruit interactions. Acta Oecologica, 83, pp.38-47. doi:
1127 10.1016/j.actao.2017.06.009

1128 Steinmetz, R., Seuaturien, N. and Chutipong, W., 2013. Tigers, leopards, and dholes in a half-empty
1129 forest: assessing species interactions in a guild of threatened carnivores. Biological Conservation, 163,
1130 pp.68-78. doi: 10.1016/j.biocon.2012.12.016

1131 Sullivan, B.L., C.L. Wood, M.J. Iliff, R.E. Bonney, D. Fink, and S. Kelling. 2009. eBird: a citizen-based bird
1132 observation network in the biological sciences. Biological Conservation, 142, pp.2282-2292. doi:
1133 10.1016/j.biocon.2009.05.006

1134 Tape, K.D. and Gustine, D.D., 2014. Capturing migration phenology of terrestrial wildlife using camera
1135 traps. BioScience, 64(2), pp.117-124. doi: 10.1093/biosci/bit018

1136 Thackeray, S.J., Henrys, P.A., Hemming, D., Bell, J.R., Botham, M.S., Burthe, S., … Mackay, E.B., 2016.
1137 Phenological sensitivity to climate across taxa and trophic levels. Nature, 535(7611), pp.241-245.
1138 doi:10.1038/nature18608

1139 Terraube, J., Villers, A., Poudré, L., Varjonen, R. and Korpimäki, E., 2017. Increased autumn rainfall
1140 disrupts predator–prey interactions in fragmented boreal forests. Global Change Biology, 23(4),
1141 pp.1361-1373. doi: 10.1111/gcb.13408

1142 Theobald, E.J., Gabrielyan, H. and HilleRisLambers, J., 2016. Lilies at the limit: Variation in plant-
1143 pollinator interactions across an elevational range. American Journal of Botany, 103(2), pp.189-197.
1144 doi: 10.3732/ajb.1500416

1145 Timberlake, T.P., Vaughan, I.P. and Memmott, J., 2019. Phenology of farmland floral resources reveals
1146 seasonal gaps in nectar availability for bumblebees. Journal of Applied Ecology, 56(7), pp.1585-1596.
1147 doi: 10.1111/1365-2664.13403

1148 Van de Pol, M., Bailey, L.D., McLean, N., Rijsdijk, L., Lawson, C.R. and Brouwer, L., 2016. Identifying the
1149 best climatic predictors in ecology and evolution. Methods in Ecology and Evolution, 7(10), pp.1246-
1150 1257. doi: 10.1111/2041-210X.12590

1151 Van Schaik, C.P., Terborgh, J.W. and Wright, S.J., 1993. The phenology of tropical forests: adaptive
1152 significance and consequences for primary consumers. Annual Review of Ecology and Systematics,
1153 pp.353-377.

1154 Varpe, Ø., 2017. Life history adaptations to seasonality. Integrative and Comparative Biology, 57(5),
1155 pp.943-960. doi: 10.1093/icb/icx123

1156 Vilela, A.A., Del Claro, V.T.S., Torezan-Silingardi, H.M. and Del-Claro, K., 2018. Climate changes
1157 affecting biotic interactions, phenology, and reproductive success in a savanna community over a 10-
1158 year period. Arthropod-Plant Interactions, *12*(2), pp.215-227. doi: 10.1007/s11829-017-9572-y

1159 Virkkala, R., Heikkinen, R.K., Leikola, N. and Luoto, M., 2008. Projected large-scale range reductions of
1160 northern-boreal land bird species due to climate change. Biological Conservation, 141(5), pp.1343-
1161 1353. doi: 10.1016/j.biocon.2008.03.007

1162 Visser, M.E., Holleman, L.J. and Gienapp, P., 2006. Shifts in caterpillar biomass phenology due to
1163 climate change and its impact on the breeding biology of an insectivorous bird. Oecologia, 147(1),
1164 pp.164-172. doi:10.1007/s00442-005-0299-

1165 Visser, M.E., Caro, S.P., Van Oers, K., Schaper, S.V. and Helm, B., 2010. Phenology, seasonal timing and
1166 circannual rhythms: towards a unified framework. Philosophical Transactions of the Royal Society B:
1167 Biological Sciences, 365(1555), pp.3113-3127. doi:10.1098/rstb.2010.0111

1168 Watt, A.D., Dixon, A.F.G., 1981. The role of cereal growth stages and crowding in the induction of
1169 alatae in *Sitobion avenae*. Ecol. Entomol. 6, 441–447. doi: 10.1111/j.1365-2311.1981.tb00636.x

1170 Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., … Heikkinen, R.K., 2013.
1171 The role of biotic interactions in shaping distributions and realised assemblages of species:
1172 implications for species distribution modelling. Biological Reviews, 88(1), pp.15-30. doi:
1173 10.1111/j.1469-185X.2012.00235.x

1174 Wolf, A.A., Zavaleta, E.S. and Selmants, P.C., 2017. Flowering phenology shifts in response to
1175 biodiversity loss. Proceedings of the National Academy of Sciences, 114(13), pp.3463-3468. doi:
1176 10.1073/pnas.1608357114/-/DCSupplemental.

1177 Yun, S., Lee, J.W. and Yoo, J.C., 2020. Host-parasite interaction augments climate change effect in an
1178 avian brood parasite, the lesser cuckoo *Cuculus poliocephalus*. Global Ecology and Conservation, 22,
1179 p.e00976. doi: 10.1016/j.gecco.2020.e00976