

Title	A review of the methods for studying biotic interactions in phenological analyses
Authors	de la Torre Cerro, Rubén;Holloway, Paul
Publication date	2020-10-30
Original Citation	de la Torre Cerro, R. and Holloway, P. (2020) 'A review of the methods for studying biotic interactions in phenological analyses', Methods in Ecology and Evolution, doi: 10.1111/2041-210X.13519
Type of publication	Article (peer-reviewed)
Link to publisher's version	https://besjournals.onlinelibrary.wiley.com/ doi/10.1111/2041-210X.13519 - 10.1111/2041-210X.13519
Rights	© 2020 British Ecological Society. This is the peer reviewed version of the following article: de la Torre Cerro, R, Holloway, P. A review of the methods for studying biotic interactions in phenological analyses. Methods Ecol Evol. 2020; 00: 1– 18, which has been published in final form at https:// doi.org/10.1111/2041-210X.13519 This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving.
Download date	2025-08-13 19:23:11
Item downloaded from	https://hdl.handle.net/10468/10893



University College Cork, Ireland Coláiste na hOllscoile Corcaigh

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

Rubén de la Torre Cerro<sup>1, 2\*</sup> and Paul Holloway<sup>1,2</sup>

1 1. Department of Geography, University College Cork, Cork, Ireland

- 2 2. Environmental Research Institute, University College Cork, Cork, Ireland
- 3 Abstract:
- 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.
- 8 2. We performed an extensive integrative review of works evaluating phenology and biotic
   9 interactions. We identified four broad categories of studies that have explored biotic
   10 interactions within phenology research: 1) spatial and temporal asynchronies, 2) biotic factors
   11 as covariates, 3) simulation studies, and 4) interaction indices.
- 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.
- 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.

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.

28 Resumen:

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.

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:
 asincronías espaciales y temporales, 2) factores bióticos como covariables, 3) estudios de
 simulaciones, 4) índices de interacciones.

39 3. Nuestra revisión muestra que los eventos fenológicos que tienen lugar durante la primavera han 40 recibido mucha más atención que la fenología de ninguna otra estación, así como el hecho de que 41 las interacciones y redes tróficas han sido exploradas más frecuentemente que interacciones de 42 facilitación o competencia. Los investigadores tienden a interpretar coexistencia entre especies 43 como una interacción biótica, sin que haya una medición directa de dicha interacción, en especial 44 en los estudios de asincronías espaciales y temporales, aunque ello también ocurre a cierto nivel 45 en el resto de las categorías. Además, también hemos encontrado una falta de examinación formal 46 en la mayoría de estudios que exploraron desajustes entre eventos fenológicos en respuesta al 47 cambio climático.

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

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

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

# 59 1. Introduction

60 Phenology is the study of cyclic and seasonal phenomena in organisms, such as leaf unfolding and 61 senescence, flowering of plants, migration events, and timing of the breeding season (Forrest & Miller-62 Rushing, 2010; Mayor et al., 2017). The outstanding impacts that phenology exerts in the functioning 63 of ecosystems and their services are well established and have fostered much research in recent 64 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 65 66 phenological impacts include the carbon sequestration potential of ecosystems (Le Quéré et al., 2017) 67 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. 68

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 73 or indirect impacts on biotic interactions (Wolf, Zavaleta & Selmants, 2017). For example, earlier 74 flowering time that overlaps with other plant species could expose plants to lower pollinator activity 75 (i.e., direct impact) as a result of competition, while also resulting in reduced herbivory pressure, 76 which has a subsequent effect on fruit onset (i.e., indirect impact) (Vilela, Del Claro, Torezan-Silingardi 77 & Del-Claro, 2018). The sensitivity of biotic interactions and interaction networks to climate change 78 means that many species and ecological networks could experience decoupling or losses of 79 interactions, which could have potentially long-standing consequences for the entire ecosystem and 80 its services (Oliver et al., 2015).

81 The phenological response to climate change drivers has been explored for many taxa, particularly for 82 plants. Earlier flowering and leaf unfolding in spring as a result of climate change are well documented 83 (Primack, Higuchi & Miller-Rushing, 2009; Rafferty & Ives, 2011; Mayor et al., 2017; Mohandass, 84 Campbell , Chen & Li, 2018). However, not all organisms respond in the same way. For example, within 85 a plant community some species might experience noticeably earlier flowering as a response to 86 variations in climatic factors, whereas other species might show low impact or remain unchanged 87 (Vilela et al., 2018). This can result in phenological mismatches at different trophic levels (Fig. 1a,d, 88 e.g. flowering time and pollinator activity; bird migration and insect development), thus threatening 89 biodiversity because of differences in phenological sensitivity to climate (Thackeray et al., 2016; 90 Kharouba et al., 2018). These phenological mismatches have been proven to be particularly important 91 for supressing specialized interactions, where higher trophic levels depend on a reduced number of 92 species in the lower levels (Both, Van Asch, Bijlsma, Van Den Burg & Visser, 2009).

93 The interactions between plant and pollinator are usually asymmetric, where a plant species depends 94 strongly on an animal species (pollinator), but the animal depends weakly on the plant (and vice versa) 95 (Bascompte, Jordano & Olsen, 2006). Asymmetric interactions usually occur within (predominantly) 96 nested networks, allowing both generalist and specialist plants to interact with both generalist and 97 specialist pollinators and thus maintain the ecosystem (Schweigher et al., 2010). Therefore, in the case

98 of (local or global) extinction of one of the interactors or asynchronies between partners, the network 99 could buffer the effect of such events, but there would be uncertainties related to how resilient 100 species might be to such changes (Fig. 1b,e). Moreover, many species initiate phenological events 101 based on species interactions, with many aphid species initiating migration based on the senescing of 102 host plants (Dixon & Glen 1971; Watt & Dixon 1981), which may or may not be captured by changes 103 in the abiotic conditions alone (Holloway, Kudenko & Bell, 2018). In addition, the effect of climate 104 change can disrupt biotic interactions in many ways, for example, turning from a favourable scenario 105 of facilitation to competitive exclusion or competence (Blois, Zarnetske, Fitzpatrick & Finnegan, 2013) 106 or by advancing or delaying phenology of species that exhibit changes in their interaction types 107 through ontogeny, which is where species shift their relationship from competition to predation, 108 facilitation to competition or herbivory to mutualism during their life cycle (Yang & Rudolf, 2010), 109 illustrated in Fig. 1c,f. Despite the complex network of interactions operating in ecosystems, the role 110 of phenological shifts on species interactions, and vice versa, remain poorly understood (Sargent & 111 Ackerly, 2008; Varpe, 2017). In a recent study, Morente-López, Lara-Romero, Ornosa and Iriondo 112 (2018) documented a great variation of within-season interactions in a plant-pollinator network in 113 which modularity (strength of groups of interacting species) was greatly influenced by species 114 phenology. Thus, evaluating the role of phenology in species interactions is vital for a better 115 understanding of biotic interactions and ecological networks.





117 Figure 1. Conceptualisation of biotic interactions under normal conditions, i.e. matching phenologies, among different trophic levels (a,b,c) 118 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) 119 interaction through the trophic network, where A interacts with B, who interacts with C, who in turn interacts with D. b) Representation of 120 obligated interactions (A+B), (B+C) where species A depends on B and species D depends on C. c) Species A favouring through facilitation, 121 under favourable conditions or a particular stage of its ontogeny, by providing nutrients, refugia or resources, the occurrence of species B, 122 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 123 perturbation, i.e. temperature rise. e) A+B interaction lost after a perturbation, i.e. habitat modification or climate change, hence A now 124 depends on C, exerting pressure on both C and D. f) Facilitation turned into competition in where A excluded all species and reduced available 125 space for B through competition.

126 There are several challenges when incorporating biotic interactions in phenology research, which may 127 have impeded its development. Firstly, there is a lack of information regarding many species 128 interactions, and even when information is available there is often a lack of replication that makes it 129 difficult to extrapolate the methodologies and results across species, environments, and models 130 (Baselaga & Aráujo, 2009). The high complexity of biotic interactions and the mechanisms involved in 131 the build-up of interaction networks, makes it difficult to model them statistically, being typically 132 parameterised in models as proxies of presence-absence of interactor partners (Palacio & Girini, 133 2018). Similarly, many interactions are unknown, hindering evaluation of biotic interactions for many 134 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).

138 Therefore, biotic interactions have been relatively neglected in phenology research (Elzinga et al., 139 2007; Morente-López et al., 2018) despite the important role they play in life cycle events. 140 Consequently, developing a generalised framework for the incorporation of biotic interactions in 141 phenology research has been difficult, meaning studies addressing interactions among different 142 species and trophic levels are rare. While methods have been proposed to investigate species 143 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 144 145 measures of biotic interactions in phenology research, models ignore one of the most important 146 ecological processes that can modify, disrupt, or decouple phenological events across ecosystems.

147 In this review we aim to investigate the methodologies used to evaluate the effect of phenological 148 change in biotic interactions and address the main challenges derived from the study of these complex 149 relations. This review aims to identify important gaps of knowledge, explore different approaches of 150 studying biotic interactions within phenology research and provide future directions, all pivot 151 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 152 153 Supplementary Information 1. Studies that have explored biotic interactions within phenology can be 154 broadly grouped into four main categories: 1) spatial and temporal asynchronies, 2) biotic factors as 155 covariates, 3) simulation studies, and 4) interaction indices. Through this we review, we aim to create 156 a generalised framework for the incorporation of biotic interactions in phenological research. Finally, 157 we end our review by exploring emerging opportunities that could be employed to investigate biotic 158 interactions within phenology research, and subsequent challenges arising from these new methods.

159

#### 160 2. Spatial and Temporal Asynchronies

161 Asynchrony among species in phenology research has predominantly focused on variations in climatic 162 factors (e.g., temperature, precipitation) that are the common drivers of phenological events of many 163 taxa, consequently leading to spatial and temporal mismatches between interlinked species (Yang & 164 Rudolf, 2010; Thackeray et al., 2016; Mayor et al., 2017). Most studies investigating temporal 165 mismatches in phenological events have focused on monitoring climatic induced changes of a single 166 species or an array of species over an extended temporal period (e.g., 30 years) that are usually linked 167 through the trophic network (Gordo & Sanz, 2006; Jones & Creswell, 2010; O'Neil et al., 2012; Dunn 168 & Moller, 2014). For example, fluctuations in bird migration trends, arrival dates, and laying dates 169 have all been documented in relation to decades of variation in temperature and precipitation in 170 wintering grounds and spring breeding areas (Gordo & Sanz, 2006; Jones & Creswell, 2010; Dunn & 171 Moller, 2014). However, studies typically rely on the assumption that earlier emergence or arrival to 172 breeding grounds will result in the mismatch of interactions that are not evaluated or quantified in 173 any way.

174 Advancements on incorporating biotic interactions within studies investigating temporal mismatches 175 have systematically modelled the relationship between species (Gordo & Sanz 2005; Burkle, Marlin & 176 Knight, 2013). For example, Gordo and Sanz (2005) used a temporal series of phenological events of 177 plants and pollinators including date of flowering and pollinator emergence over a 50-year period in 178 order to infer decoupling of plant-pollinator interactions. Climate induced changes in plant phenology 179 were estimated using dimension reduction models (e.g., two dynamic factor analyses) to identify 180 common temporal patterns within plant phenological events. Advancing on this, the authors 181 employed regression analyses to determine patterns of change on the timings of phenological events 182 (e.g., insect emergence, bird migration) showing advancement on insect emergence related to 183 advanced flowering but the interaction among both was not explicitly analysed. Figure 2a highlights a 184 hypothetical visualisation of such results, with the fitted line representing a linear model for showing

the trend on timing (asynchronies) of two phenological events, plant flowering and insect emergence.
The dotted line represents documented differences in Julian days between the two studied
phenological events, extracted from independent datasets, and evidences the lack of direct method
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.



216

217 Figure 2. Different approaches to modelling biotic interactions from proxies. A) Modelled elapsed days between date of insect emergence 218 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 219 and Sanz (2005). Black dots represent positive or negative differences between timing on phenologies of the two taxa, dotted line reflects 220 trends in variations of temporal asynchronies, fitted line represents a linear model of the tendency of these asynchronies. B) 221 Conceptualization of an experimental network of plant-pollinator interactions over time in which an assemblage of plants (species A, B, C, 222 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 223 B manipulated to flower earlier than their current mean flowering date, C and D manipulated for a delayed flowering and E remained 224 unchanged according its current flowering date. Pollinator visits (species 1 to 5) are documented over time, light grey squares represent 225 plant-pollinator interactions and dark grey squares represent low rate pollinator visitation. C) Trends of phenological change, in comparison 226 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 227 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).

230 Application of temporal asynchronous analysis requires long-term time-series data, and due to the 231 resources required to collect such data, this research is often restricted spatially to very localised sites. 232 Subsequently, studies are beginning to use species distribution models (SDMs) to quantify spatial and 233 temporal asynchrony in phenology. SDMs use information regarding the locations of organisms 234 together with geospatial environmental parameters to identify species-environment relationships and 235 use these to extrapolate habitat suitability into novel space and time (Elith & Leathwick, 2009). While 236 phenology has not been a traditional application of SDM research, in part due to their static 237 representation of a species niche (Peterson et al., 2011), studies are beginning to emerge (Porfirio, 238 Harris, Stojanovic, Webb & Mackey 2016; Yun, Lee & Yoo, 2020). For example, Yun et al. (2020) 239 modelled the distribution of the cuckoo (brood parasite) and 12 passerine birds (host species) to 240 ascertain the amount of spatial overlap in their distributions under changing climates. By quantifying 241 the difference in spatial area, the authors identified a decrease in suitable habitat for all species, but 242 also a decrease in the amount of overlap between cuckoos and their hosts, subsequently impacting 243 breeding phenology.

244 Therefore, the need for a spatial consideration in any phenological research investigating asynchrony 245 among species is key, as changes in timing may occur differently across ecoregions, ranges, and 246 altitudes. For example, Benadi, Hovestadt, Poethke and Blüthgen (2014) used an altitudinal gradient 247 as proxy for expected climate change over time, to evaluate the degree of synchrony between 248 specialised flower visitors and their main plant resource. By modelling plant-insect phenological shifts 249 among different altitudes with linear mixed-effects models, the authors demonstrated that 250 consistency of specialised pollinators and phenological synchrony with their main source was not 251 maintained at different altitudes.

252 Studies investigating spatial and temporal mismatches among species have generally focused on 253 spring phenology (Visser et al., 2006; Primack et al., 2009; Mayor et al., 2017; O'Neill et al., 2012; 254 Bartomeus et al., 2011; Phillimore, Leech, Pearce-Higgins & Hadfield, 2016), while studies addressing 255 autumn phenology are scarcer (Gordo & Sanz, 2005; Gordo & Sanz, 2006; Gallinat, Primack & Wagner, 256 2015). Although evidence of advanced spring phenology is widespread (Heghland et al., 2009; O'Neill 257 et al., 2012; Phillmore et al., 2016), this trend is unclear for autumn phenology and the lack of 258 comparative studies makes it difficult to discriminate patterns during this season (Gordo & Sanz, 259 2005). Moreover, in many of the aforementioned studies, interactions were considered to be static 260 among species, as well as expected to change linearly with the abiotic conditions. The expected linear 261 change in such cases is realistic until some point, but species will not advance their phenology 262 endlessly. Thus, the nature of relationships, such as type and strength, might change along with abiotic 263 conditions, meaning the selection of parameters need to be appropriate to the system under study in 264 order to account for such factors (e.g., non-linear relationships - Austin, 2007). Consequently, under 265 the current climate change scenarios (IPCC, 2018), phenological mismatches have the potential to 266 deeply impact biotic interactions, therefore long-term spatially and temporally explicit phenological 267 studies could help to improve management actions to preserve the integrity of interaction networks.

#### 268 **3. Biotic Factors as Covariates**

269 Despite their relevance, biotic factors have been relatively neglected in phenological studies, 270 particularly when compared to the historical use of abiotic drivers (Thackeray et al., 2016; Wolf et al., 271 2017); however, studies have begun to incorporate them as additional explanatory variables or 272 covariates in statistical models. Biotic variables are often included in the models to investigate the role 273 of species interactions on phenological events, predominantly using data obtained from manipulative 274 field studies (e.g., visual identification among transects, capture-recapture, and monitoring of nests -275 Visser et al., 2006). Generally, interactions through trophic levels are documented more often since 276 impacts on one of the interactors of these obligated or specialised networks, in which one species 277 directly depends on other as a food source, will lead to a response on the other partner. For example, 278 by evaluating differences in the onset of forage species (either herbivores or predators), the impact 279 of any phenological mismatch in the reproductive success of forager populations can be estimated 280 (Visser et al., 2006; Post & Forchhammer, 2008). These manipulations aim to account for the effect of 281 temporal or spatial changes in environmental conditions, phenological events or biotic interactions. 282 For example, Martin and Maron (2012) tested the effect of reduction in snow cover, given a 25-year 283 period of snowfall decline, as a factor influencing bird and plant population declines through increased 284 herbivory and nest predation. The authors studied changes in plant assemblages for herbivory-285 prohibited (i.e., simulated snow cover) and herbivory-exposed sites finding that reduction in snow 286 cover exposed plant assemblages to higher herbivory pressure, leading to declines in bird populations 287 due to increased nest predation. However, an increase in plant and bird populations (including a 288 reduced nest predation) was documented in herbivory-prohibited areas.

289 Research has also addressed the importance of the spatial dimension of phenological shifts. For 290 example, larger shifts in phenology (e.g., longer mismatches in Julian days) have been related to higher 291 latitudes and elevations, which act as a proxy for increases in global temperature (Chmura et al., 2019). 292 Altitudinal gradients serve to illustrate climate change effects as conditions in upward populations are 293 usually associated to pre-climate change scenarios while downward populations serve as example of 294 the conditions that upward populations would experience in the future (Alexander, Diez & Levine 295 2015). Although some of the reviewed studies monitored biotic parameters, there is still a marked 296 importance of abiotic factors, with studies typically testing several within models i.e. factors such as 297 temperature increase and nutrient enrichment on specialised trophic interactions (Lu, Siemann, Shao, 298 Wei & Ding, 2013; de Souza Laurindo, Gregorin & Tavares, 2017; Terraube, Villers, Poudré, Varjonen, 299 & Korpimäki, 2017). For example, Terraube et al. (2017) showed the importance of climate factors and 300 forest management on the foraging success of an owl species by using field data and GLMMs. The 301 authors documented a trend of decreased prey biomass stored in nests related to increasing rainy 302 days and days with frost, which in turn is expected to affect the biomass and fitness of the target owl 303 species. However, despite the importance of incorporating both abiotic and biotic factors on 304 interactions, few experimental studies have actually tested this within a phenology context.

305 Alexander et al. (2015) exposed plants to different treatments of abiotic conditions and presence of 306 expected interactor species in order to determine if competition or facilitation would dominate plant 307 assemblages under predicted climate change. By using mixed-effect models and GLMs, the effect of 308 presence of competitors on the transplanted individuals was estimated, showing that under warmer 309 conditions the identity of the competitor had a significant effect on the transplanted individuals' 310 success. Wolf et al. (2017) carried out experiments manipulating biodiversity of plant assemblages to 311 reflect random or realistic biodiversity loss, in terms of the number and identity of species. Their aim 312 was to test for the effect of biotic interactions on the timing of flowering peak (highest flower 313 abundance per species and plot were used as a surrogate variable for time of flowering) of each 314 species. In this case, plots with low plant diversity showed earlier flowering, while flowering peaks 315 between species were more dispersed in high diversity treatment plots than in monocultures. Other 316 studies have begun to test both abiotic and biotic factors in experimental settings (Bresson, 317 Varoquaux, Bontpart, Touraine & Vile, 2013; Koyama & Tsyuzaki, 2013), with studies manipulating 318 environmental conditions useful to determine changes in phenology and the evolution of specialized 319 interactions under predicted climate change conditions. Moreover, experimental works manipulating 320 abiotic and biotic conditions in order to evaluate phenological response and adaptive success are 321 performed by translocating individuals (usually plants) to new areas (within and beyond) their 322 distributional range, or through lab manipulation (Lau & Lennon 2012). Thus, the inclusion of biotic 323 interactions in phenology research could change the statistical response, effect, and importance of 324 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.

336 Conversely, there is usually a lack of replication in most field or manipulative studies. For example, 337 even when biotic interactions are statistically proven to be one of the main explanatory variables 338 within a system, the lack of replication over time and the scarcity of comparative studies might lead 339 to misinterpretations. For instance, Theobald, Gabrielyan and Hillerislambers (2016) demonstrated 340 the importance of pollinator-mediated seed production of a montane plant species. The authors tried 341 to investigate the role of pollinators for determining the range limit of the plant (through pollen 342 limitation), suggesting the importance of different pollinator groups for reproductive success; 343 however, factors determining the species' range limit could not be separated from plant interannual 344 variations. Further, some studies evaluate small populations which highlight the fact that small sample 345 sizes might mask the effect of other possible factors and lead to erroneous interpretations (Post & 346 Forchhammer, 2008; Benadi et al., 2014). Furthermore, although most of these experimental studies 347 include environmental variables, given the scale and dimension of these open mesocosm experiments, 348 there might be environmental variables that are not considered and could explain some of the 349 statistical variation found in them (Wolf et al., 2017), compounding our ability to interpret such biotic 350 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 351 352 conditions that are of great importance for the phenology of plant and pollinators (Makoto et al., 2014). 353

354

355

## 356 4. Simulation models

357 Simulation models are statistical models where one or more parameters are manipulated in order to 358 elicit predictions in the response of the ecological factor under consideration (Chuine & Régnière, 359 2017). These factors could include the presence or abundance of a species, the spatial or temporal 360 changes of a particular phenological event, and the persistence of a biotic interaction. These models 361 have been used to explore a wide array of phenological events, such as co-occurrence of interactor 362 species influencing pollination interactions (CaraDonna et al., 2017), the role of plant-pollinator 363 synchrony in community assemblages (Bartomeus et al., 2013) and the role of changing phenology on 364 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, 365 366 2008; Dullinger et al., 2012), during the development of this review we found very few papers where 367 simulations investigated the effect of climate change on phenological events or biotic interactions 368 (Memmott, Craze, Waser & Price, 2007; Araújo, Rozenfeld, Rahbek & Marquet, 2011; Roberts, Tansey, 369 Smithers & Phillimore, 2015; Bateman et al., 2016; Goberville et al., 2016; Schleuning et al., 2016).

370 Simulation models have been used to predict the evolution of ecological networks, by modelling 371 predicted phenological mismatches among interactor partners, as well as extracting interactor species 372 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 373 374 networks, species sensitivity to climate change driven coextinctions can be estimated. For example, 375 Schleuning et al. (2016) modelled the effects of climate change on ecological networks, and 376 subsequently simulated secondary species extinction as a consequence of the sequential loss of plant 377 and animal species. Network sensitivity was then quantified ranging from no secondary species going 378 extinct to all species. Simulations showed that specialized animals would suffer greater impact than 379 plants from secondary extinctions in mutualistic networks due to climate change. Moreover, 380 applications of simulation models can be used to construct networks of co-occurrences that serve as

381 proxies of interactions or to infer biotic interactions from co-occurrence patterns (Araújo et al., 2011; 382 Araújo & Rozenfield, 2014). For instance, Araújo and Rozenfield (2014) created a point-process model 383 from co-occurrences to infer biotic interactions and to evaluate their relevance at different spatial 384 scales. Spatial overlap (attraction or repulsion) together with probability of occurrence of interactors 385 in space was interpreted as a signal of biotic interactions that were scored according to the number 386 of times species co-occurred within cells in order to estimate their spatial importance. Their results 387 suggested that the effect of negative interactions was clearer at fine scales and diluted at coarse scale 388 whereas positive interactions (mutualism, commensalism) and those related to consumer-resources 389 were scale independent.

390 Simulations have also been useful to model species distributional limits and probability of survival 391 beyond geographical ranges. For example, Benning, Eckhart, Geber and Moeller (2019) used field 392 experiments to train simulations on plant fitness in the presence and absence of herbivory. 393 Simulations were tested by exploring the impact of herbivory on the fitness and survival of a 394 Californian annual plant species, investigating delayed phenology and the probability of survival 395 beyond its geographic range. When climate conditions were advantageous (i.e. higher precipitation) 396 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 397 398 biotic relationship was excluded, although not high enough to support population establishment and 399 growth. While this study explored antagonistic interactions, mutualistic interactions within networks, 400 such as pollination, were addressed the most frequently across all simulation studies (Memmott et 401 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

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

409 However useful simulations are, these approaches face similar challenges, such as the lack of robust 410 data on interaction networks, as well as sensitivity to the lack of knowledge about rare interactions 411 (Olito & Fox, 2015). In many cases, the lack of basic knowledge on species biology and biotic 412 interactions could lead to erroneous predictions or interpretations that under- or over-estimate the 413 power of these models (Memmott et al. 2007). Additionally, considering a network of interactions as 414 a sealed system is often a caveat of these methodologies. For example, when modelling species 415 extinctions, these models are performed assuming that no new interactions are entering the system, 416 which can undermine the power of the model as this is not entirely realistic. Moreover, despite the 417 importance of phenology structuring networks of interactions (Morante- López et al., 2018), studies 418 modelling biotic interactions frequently ignored the phenological dimension of these (Araújo et al., 419 2011; Araújo & Rozenfield, 2014; Schleuning et al., 2016). Although there are some advances in the 420 field of predictive models of biotic interactions, in particular the novel approach of Graham and 421 Weinstein (2018) to develop models predicting species interactions, the lack of a robust methodology 422 on this topic limits the use to elaborate predictions on species interactions.

## 423 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 431 compared the number of visits of a pollinator (later pooled to taxonomic groups) to a plant species,
432 and then further comparing visits to total flower resources and a null model of expected visits. The
433 authors demonstrated different degrees of specialisation among taxonomic groups of pollinators and
434 the importance of floral traits (tube length) rather than plant species identify.

435 Novel advances on field monitoring of phenology, particularly using new technology, are leading to 436 the development of community interaction indices (Buxton et al., 2016; Oliver et al., 2018). For 437 example, Buxton et al. (2016) used a novel acoustic index, developed by Pieretti, Farina and Morri 438 (2011), to monitor spring and winter phenology of songbirds. The acoustic complex index (ACI) 439 measures the vocalizations produced on an avian community and poses as an important tool for the 440 study of phenological events at large spatiotemporal scales. This index is calculated as the differences 441 in sound pressure level among adjacent seconds of the recorded period divided by the total value of 442 sound pressure level for the recorded band. Acoustic recorders were placed in different areas in order 443 to acquire different ACI values over a three-year period. ACI values were compared with species-444 specific acoustic analyses to determine changes in the acoustic landscape produced by the arrival of 445 migrant birds. Further, the relationship between species beta-diversity and ACI was documented with 446 differences in values among seasons calculated through Bayesian change point analyses and GLMMs. 447 Abrupt changes in phenology were recorded in spring, but these were not as prominent during the 448 autumn season, partially due to extreme weather events obscuring the acoustic data. Thus, potential 449 of acoustic recorders to continually monitor the phenological landscape offers a unique insight in 450 measuring how phenology (and subsequent biotic interactions) change over time (Deichmann et al., 451 2018), and while several novel challenges are associated with the technology (Shonfield & Bayne, 452 2017) their use offers a means to establish a holistic monitoring system that can integrate both local 453 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<sub>i</sub>) and multiple traits (V<sub>i</sub>) 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<sub>i</sub>) 459 that employed distance matrices, weighted means, and random distances (among other parameters). 460 Simultaneously they created the trait volume index (V<sub>i</sub>) exploring groups of flower traits that could 461 influence pollinator preferences, calculated as the product of all individual S<sub>i</sub> of each tray by each 462 volume V<sub>i</sub> 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 frameworks for the study of phenology (Visser et al., 2010) and the shifts of phenology-ontogeny (Yang 478 479 & 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 within phenology (Fig. 3), apportioning this into two interconnected factions where research is aimed
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.



549 Figure 3. Framework illustrating the conceptualisation and modelling of biotic interactions in phenology research. Conceptualisation occurs 550 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 551 time, emergence time, first flight, bud burst, etc., then the interactions of interest (2), e.g., pairwise or network, inter or intra-specific, and 552 type of interaction i.e. trophic (herbivory, predation, etc.), positive (facilitation, mutualism, commensalism), negative (competence, 553 amensalim) or neutral. Then researchers must consider the dimension (3) of study, which accounts for the different spatial and temporal 554 extent of the variables that will shape the modelling process. Finally, this will lead to the measurement of biotic interactions (4), in which 555 we discriminate between indirect (4a-b) and direct (4c-e) measurements. Indirect measurements include those that have been quantified 556 from co-existence records (4a) or parameters that use proxies or covariates (4b), including presence-absence and functional traits. Direct 557 measurements include parameters directly monitored in the field (4c), including pollinator visitation, parameters from experimental 558 treatments (4d), including manipulated vs non-manipulated individuals, and estimates (rates) as covariates (4e), including predation or 559 herbivory rates. We propose that indirect measurements should proceed as co-existence studies, while direct measures should proceed as 560 interaction studies. The modelling of biotic interactions and co-existence studies occurs during points 5-7. There are three main ways in 561 which the study variables are often represented (5): Activity length (purple box) i.e. differences in arrival date, emergence date, flowering 562 time, typically measured in Julian or calendar days. Parameters (green box), when variables of study are ecological measurements such as 563 richness, functional traits, distribution of interactors, presence - absence data, etc., and Rates (blue box), when the variables are estimated 564 as a measurement of a biotic interaction, e.g. predation rate, parasitism rate, pollination success. The selected variables together with the 565 abiotic variables of interest are then modelled (6) using the approaches applicable for the study of biotic interactions, leading to (7) the four 566 identified categories where coloured quadrats (purple, blue and green) in the lower box symbolize the type of variable representation 567 typically incorporated in the different modelling approaches.

568 **7 Emerging Opportunities and Challenges** 

#### 569 7.1 Spatial Modelling through SDM

570 Accounting for the complexity that phenological events pose at both spatial and temporal scales is 571 difficult. With advances in data collection, SDMs (as described in section 2) are now being 572 parameterised more readily with temporally explicit variables (e.g., normalized difference vegetation 573 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 574 575 projections being used as estimates for phenological events. For example, Gschweng, Kalko, Berthold, 576 Fiedler, and Fahr (2012) matched telemetry data with meteorological and habitat data to project 577 monthly distributions of the Eleonara's falcon in Madagascar, identifying seasonal patterns of 578 distributions, and relating this to the timing of migration events. Distribution projections could

579 theoretically be generated at finer (e.g., daily, weekly, or monthly) timescales, which may capture 580 important information regarding the relationship between phenological events and species 581 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 582 583 and environmental data. The increase in habitat suitability for barn swallows in April aligns with their 584 migration, and supports the premise that SDMs parameterised on averaged climate variables (e.g., 585 mean temperature) have often failed to capture the actual variability that species experience in short 586 time periods which drive changes in the spatial distributions across the life cycle (Eyre, Rushton, Luff 587 & Telfer, 2005).



Figure 4. Example of monthly habitat suitability 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).

600 Several recent and thorough reviews within SDM explore the role of biotic interactions in model 601 parameterisation using both correlative and joint-SDM (e.g., Wisz et al., 2013; Dormann et al., 2018; 602 Peterson et al., 2020), and as such it is not our aim to duplicate efforts. Instead, we highlight challenges 603 and frontiers of incorporating biotic interactions within SDM and identify where phenological research 604 could learn from this burgeoning field. The inclusion of biotic parameters (representing interactions 605 or co-existence) in SDMs generally leads to improvement of predictive power of the models (Atauchi 606 et al., 2017; Palacio & Girini, 2018), however, the fact that a model integrates biotic parameters does 607 not always increase model accuracy (e.g., Holloway, 2018). In some cases when the considered biotic 608 interactors are highly correlated to abiotic parameters, for example climatic conditions that determine 609 presence of a particular species, the inclusion of biotic factors in model parameterisation might result 610 in multicollinearity or show no improvements of SDMs due to the overarching influence of abiotic 611 conditions (Silva et al., 2014). Recently, Raath, Le Roux, Veldtman and Greve (2018) compared four 612 methods of incorporating biotic factors, by using different representations of host-plant distributions 613 in SDMs of two silk moth species in sub-Saharan Africa. They found that inclusion of moth-host plant 614 interactions in SDM greatly affected the predictive ability of the models, yet there was inconsistency 615 among biotic representation. The inclusion of temporally explicit quantified biotic factors in SDM is 616 rare (although note Mezquida, Svenning, Summers & Benkman (2018) who recorded the spatial 617 timings of seed fall for European Scots pine and included this as a covariate in an SDM projecting the 618 European distribution of crossbills), meaning studies have to rely on proxies for interactions within 619 SDM. Thus, relevance of interactions and how interactions are represented in model parameterisation 620 can shape the resulting outputs. With biotic representation a key component of our conceptual 621 framework (Fig. 3), this subsequently warrants further research to investigate whether such patterns 622 exist across multiple interactors and trophic levels within phenology.

#### 623 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 627 (Hebblewhite & Haydon, 2010), having been used to capture information on phenological interactions, 628 such as mating, boundary patrolling, and hunting (Long & Nelson 2013; Benhamou, Valeix, Chamaillé-629 Jammes, Macdonald & Loveridge, 2014 ; Long, Nelson, Weeb & Gee, 2014). Despite this advancement 630 in technology, similar issues relating to the direct estimate of intra- and inter-species-specific 631 interactions persists. For example, Miller (2012; 2015) tested several commonly implemented indices 632 of dynamic interactions for brown hyenas in Botswana alongside a null model of movement. The 633 results suggested that the use of 'expected' values in their generation produced inconsistent results, 634 which led to both Type I and II errors in the model interpretation. The general consensus has been 635 that such indices perform well at identifying no interaction between individuals; however, the majority 636 of these models use proximity in space and time (i.e. co-existence) to infer interaction, meaning similar 637 issues of interaction contextualisation persist. However, indirect interactions through smell or sight 638 that impact movement behaviours (e.g., leading, following) are difficult to model due to the 639 hierarchical nature of the processes, and may be considered as 'no interaction' in established indices 640 due to the spatial and temporal asynchrony. New methods that consider the potential path area of 641 movement trajectories in temporally asynchronous space are being developed that allow for such 642 interactions to be quantified (Hoover, Miller & Long 2020).

643 Similarly, camera traps have also been used to capture information on phenology (e.g., Graham, 644 Riordan, Yuen, Estrin & Rundel, 2010; Tape & Gustine 2014; Alberton et al., 2017), allowing the 645 examination of community structures and interspecific interactions (Steinmetz, Seuaturien & 646 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 180 647 648 camera traps to investigate interactions among raptor species (i.e. bald and golden eagle) in eastern 649 continental USA in relation to their migration phenology and subsequent interactions. By analysing 650 the presence of raptors in more than 2.5 million images, the authors found that bald and golden eagles 651 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 652

653 of camera traps to capture observed interactions is a primary advantage to the technology. However, 654 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 655 necessarily confirm that the animals actually ate the fruit. Therefore, despite the potential of such 656 657 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 658 659 and time as well as direct interactions. New methods of quantifying these interactions, through image 660 analysis, acoustic signals, and movement parameters will subsequently be needed to ascertain in what 661 instances interactions can be recorded.



662

663 Figure 5. Illustration of co-existence between species versus biotic interactions using technology including camera traps, acoustic recorders, 664 and telemetry data. Image captured from a camera traps in the Ghanzi region of Botswana, showing presence of black-back jackal and 665 hooded vultures a) in the same location at same time, not interacting and b) an interaction (competition) between two individuals. Photo 666 credit Thoralf Meyer. Audiograms from acoustic recorders (AudioMoth) (Hill et al., 2018) in Cork, Ireland, showing waveforms of recorded 667 calls (green line), blue lines are the fragment of the calls analysed identifying vocalization, with SoundID (Boucher, 2014), c) illustrating co-668 existence, vocalizations of various individuals of two different corvidae species, jackdaw and rook, where no apparent interaction was taking 669 place and d) illustrating interaction (competition) between jackdaws and rooks, with the audiogram reporting corresponding patterns for 670 alarm and territorial calls. Global positioning system (GPS) of Burchill's zebra in Botswana, showing e) coexistence and f) interaction (herding) 671 between individuals over a 24-hour period. Zebra data from Bartlam-Brooks et al. (2013a,b) via Movebank (2013), visualised in DYNAMO-672 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

699 and Bidner (2016) used a combination of camera traps, acoustic recorders, and telemetry data to 700 investigate the interactions between vervet monkeys and leopards in Kenya. Alarm calls recorded 701 through the acoustic recorders revealed that these occurred most frequently at dusk and dawn, while 702 camera traps revealed that leopards approached vervets most frequently at night when alarm-calls 703 were initiated less. Telemetry data then identified the direction of movement of leopards associated 704 with corresponding alarm calls from the acoustic devices, finding that when alarm calls were present, 705 leopards moved quickly away up to 200m. Such a novel study identifies a successful framework for 706 overcoming the individual limitations of each of the technologies, allowing interactions to be 707 confirmed. However, the authors did not generate any quantification of these interactions, providing 708 a qualitative description of the measurements. Such approaches could be extended to explore 709 interactions directly related to phenological events, such as breeding success for prey species. Reviews 710 are emerging that explore the utility of combining acoustic recorders with camera traps (Buxton et al., 711 2016), and technological advancements are combining GPS collars with remote cameras to provide 712 context to interaction (Hebblewhite & Haydon 2010). The International Cooperation for Animal 713 Research Using Space (ICARUS) has also recently launched, aiming to utilise satellite and tracking 714 technology to observe the movement of small animals, providing a global approach to animal 715 movement, which will undoubtedly provide new insights informing phenology and biotic interactions. 716 Marion et al. (2020) provide an up-to-date review of methods for studying human-wildlife interactions 717 using camera traps and telemetry data, with recommendations potentially applicable to studying 718 biotic interactions in phenology research. It is evident that such interdisciplinary approaches are 719 needed in this emerging research field.

720 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 724 processes, and vice versa. While studies investigating biotic interactions in phenology are relatively 725 scarce, several studies across disparate disciplines have undertaken research, and can be broadly 726 grouped into four main categories: 1) spatial and temporal asynchronies, 2) biotic factors as 727 covariates, 3) simulation studies, and 4) interaction indices. Spatial and temporal mismatch studies 728 have typically used historical datasets to infer changes in biotic interactions that are not measured 729 from co-occurrence records (Gordo & Sanz, 2005) or SDM projected into future space and time to 730 investigate changes in distributions among interactor species (Yun et al., 2020). Biotic factors as 731 covariates studies have focused on trophic or obligated interactions since any change in one interactor 732 is expected to have impact on the other (Post & Forchamer, 2007). However, experimental studies 733 testing both abiotic and biotic factors are still rare (Alexander et al., 2015). Simulation studies of 734 phenological events and biotic interactions are rare and have mainly been developed to test for 735 changes in phenological events under different climatic scenarios (Bateman et al., 2016) or to evaluate 736 changes in ecological networks by removing biotic components (Schleuning et al., 2016). Novel 737 approaches developing interaction indices can help to develop new methodologies to document 738 phenological events at broad regional scales (Buxton et al., 2016) as well as providing new insights for 739 the monitoring of biotic interactions. Finally, we introduce a new framework that apportions biotic 740 interactions into two interconnected factions where research is aimed towards 1) conceptualising 741 biotic interactions within phenology and 2) modelling biotic interactions within phenology. Such a 742 framework should provide researchers and practitioners with a basis to investigate interactions and 743 co-existence successfully and robustly within the wider field of phenology.

### 744 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.

748

#### 749 9. Acknowledgements

We would like to thank the anonymous reviewers and editors for their constructive and valuable comments. We would also like to thank Fiona Cawkwell, Javier delBarco-Trillo, Gourav Misra, and Astrid Wingler, for their comments and suggestions during early stages of this review. This project is funded under the EPA Research Programme 2014-2020 (PhenoClimate 2018-CCRP-MS.54). The EPA Research Programme is a Government of Ireland initiative funded by the Department of the Environment, Climate and Communications. It is administered by the Environmental Protection Agency, which has the statutory function of co-ordinating and promoting environmental research.

## 757 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).

## 761 **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.16000587.2011.06919.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

- Atauchi, P.J., Peterson, A.T. and Flanagan, J., 2018. Species distribution models for Peruvian
  plantcutter improve with consideration of biotic interactions. Journal of Avian Biology, 49(3), pp.jav01617. doi:10.1111/jav.01617
- Austin, M., 2007. Species distribution models and ecological theory: a critical assessment and some
  possible new approaches. Ecological Modelling, 200(1-2), pp.1-19.
  doi:10.1016/j.ecolmodel.2006.07.005
- Bartlam-Brooks, H.L.A., Beck, P.S., Bohrer, G. and Harris, S., 2013a. In search of greener pastures –
  using satellite images to predict the effects of environmental change on zebra migration. Journal of
  Geophysical Research: Biogeosceinces, 188, 1–11. doi:10.1002/jgrg.20096
- Bartlam-Brooks, H.L.A. and Harris, S., 2013b. Data from: in search of greener pastures: using satellite
  images to predict the effects of environmental change on zebra migration. *Movebank Data Repository*.
  doi:10.5441/001/1.f3550b4f
- Barrett, B., Nitze, I., Green, S. and Cawkwell, F., 2014. Assessment of multi-temporal, multi-sensor
  radar and ancillary spatial data for grasslands monitoring in Ireland using machine learning
  approaches. Remote Sensing of Environment, 152, pp.109-124. doi: 10.1016/j.rse.2014.05.018
- Bartomeus, I., Ascher, J.S., Wagner, D., Danforth, B.N., Colla, S., Kornbluth, S. and Winfree, R., 2011.
  Climate-associated phenological advances in bee pollinators and bee-pollinated plants. Proceedings
  of the National Academy of Sciences, 108(51), pp.20645-20649. doi: 10.1073/pnas.1115559108//DCSupplemental.
- Bartomeus, I., Park, M.G., Gibbs, J., Danforth, B.N., Lakso, A.N. and Winfree, R., 2013. Biodiversity
  ensures plant–pollinator phenological synchrony against climate change. Ecology Letters, 16(11),
  pp.1331-1338. doi: 10.1111/ele.12170
- Bascompte, J., Jordano, P. and Olesen, J. M., 2006. Asymmetric coevolutionary networks facilitate
  biodiversity maintenance. Science, 312, pp.431-433. doi: 10.1126/science.1123412

Baselga, A. and Araújo, M.B., 2009. Individualistic vs community modelling of species distributions
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

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
- Bateman, B.L., Pidgeon, A.M., Radeloff, V.C., VanDerWal, J., Thogmartin, W.E., Vavrus, S.J. and
  Heglund, P.J., 2016. The pace of past climate change vs. potential bird distributions and land use in
  the United States. Global Change Biology, 22(3), pp.1130-1144. doi: 10.1111/gcb.13154
- Benadi, G., Hovestadt, T., Poethke, H.J. and Blüthgen, N., 2014. Specialization and phenological
  synchrony of plant–pollinator interactions along an altitudinal gradient. Journal of Animal
  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
- Benhamou, S., Valeix, M., Chamaillé-Jammes, S., Macdonald, D.W. and Loveridge, A.J., 2014.
  Movement-based analysis of interactions in African lions. Animal Behaviour, 90, pp.171-180. doi:
  10.1016/j.anbehav.2014.01.030
- Blanchet, F.G., Cazelles, K. and Gravel, D., 2020. Co-occurrence is not evidence of ecological
  interactions. Ecology Letters, 23, pp.1050–1063. doi: 10.1111/ele.13525
- Blois, J.L., Zarnetske, P.L., Fitzpatrick, M.C. and Finnegan, S., 2013. Climate change and the past,
  present, and future of biotic interactions. Science, 341(6145), pp.499-504. doi:
  10.1126/science.1237184

- Both, C., Van Asch, M., Bijlsma, R.G., Van Den Burg, A.B. and Visser, M.E., 2009. Climate change and
  unequal phenological changes across four trophic levels: constraints or adaptations?. Journal of
  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.
- Bresson, J., Varoquaux, F., Bontpart, T., Touraine, B. and Vile, D., 2013. The PGPR strain *Phyllobacterium brassicacearum* STM 196 induces a reproductive delay and physiological changes that result in improved drought tolerance in *Arabidopsis*. New Phytologist, 200(2), pp.558-569. doi: 10.1111/nph.12383
- Brzostek, E.R., Dragoni, D., Schmid, H.P., Rahman, A.F., Sims, D., Wayson, C.A., ... Phillips, R.P., 2014.
  Chronic water stress reduces tree growth and the carbon sink of deciduous hardwood forests. Global
  Change Biology, 20(8), pp.2531-2539. doi: 10.1111/gcb.12528
- Burkle, L.A., Marlin, J.C. and Knight, T.M., 2013. Plant-pollinator interactions over 120 years: loss of
  species, co-occurrence, and function. Science, 339(6127), pp.1611-1615. doi:
  10.1126/science.1232728
- Buxton, R.T., Brown, E., Sharman, L., Gabriele, C.M. and McKenna, M.F., 2016. Using bioacoustics to
  examine shifts in songbird phenology. Ecology and Evolution, 6(14), pp.4697-4710. doi:
  10.1002/ece3.2242
- Camargo-Sanabria, A.A. and Mendoza, E., 2016. Interactions between terrestrial mammals and the
  fruits of two neotropical rainforest tree species. Acta Oecologica, 73, pp.45-52.
  https://doi.org/10.1016/j.actao.2016.02.005
- CaraDonna, P.J., Petry, W.K., Brennan, R.M., Cunningham, J.L., Bronstein, J.L., Waser, N.M. and
  Sanders, N.J., 2017. Interaction rewiring and the rapid turnover of plant–pollinator networks. Ecology
  Letters, 20(3), pp.385-394. doi: 10.1111/ele.12740

- Chmura, H.E., Kharouba, H.M., Ashander, J., Ehlman, S.M., Rivest, E.B. and Yang, L.H., 2019. The
  mechanisms of phenology: the patterns and processes of phenological shifts. Ecological Monographs,
  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., ...
- 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
- Diehl, R.H., Larkin, R.P. and Black, J.E., 2003. Radar observations of bird migration over the Great
- Lakes. The Auk, 120(2), pp.278-290. doi: 10.1093/auk/120.2.278
- Dixon, A.F.G., Glen, D.M., 1971. Morph determination in the bird-cherry oat aphid, *Rhopalosiphum 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
- false conclusions. Global Ecology and Biogeography, 27(9), pp.1004-1016. doi: 10.1111/geb.12759
- B63 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

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

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

- eBird. 2017. eBird: An online database of bird distribution and abundance [web application]. eBird,
  Cornell Lab of Ornithology, Ithaca, New York. Available: http://www.ebird.org. (Accessed: January 30,
  2020).
- Elith, J. and Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction
  across space and time. Annual review of Ecology, Evolution, and Systematics, 40, pp.677-697.
  https://doi.org/10.1146/annurev.ecolsys.110308.120159
- Eyre, M.D., Rushton, S.P., Luff, M.L. and Telfer, M.G., 2005. Investigating the relationships between
  the distribution of British ground beetle species (Coleoptera, Carabidae) and temperature,
  precipitation and altitude. Journal of Biogeography, 32(6), pp.973-983. doi:10.1111/j.13652699.2005.01258.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

- Forrest, J. and Miller-Rushing, A.J., 2010. Toward a synthetic understanding of the role of phenology
  in ecology and evolution, 365, pp.3101–3112. doi:10.1098/rstb.2010.0145
- 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
- change and the ash dieback crisis. Scientific Reports, 6(1), pp.1-9. doi: 10.1038/srep35303

- Gordo, O. and Sanz, J.J., 2005. Phenology and climate change: a long-term study in a Mediterranean
  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
- 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
- Biology, 16(11), pp.3014-3023. doi: 10.1111/j.1365-2486.2010.02164.x
- Graham, C.H. and Weinstein, B.G., 2018. Towards a predictive model of species interaction beta
  diversity. Ecology Letters, 21(9), pp.1299-1310. doi: 10.1111/ele.13084
- Gschweng, M., Kalko, E.K., Berthold, P., Fiedler, W. and Fahr, J., 2012. Multi-temporal distribution
  modelling with satellite tracking data: predicting responses of a long-distance migrant to changing
  environmental conditions. Journal of Applied Ecology, 49(4), pp.803-813. doi:0.1111/j.13652664.2012.02170.x
- He, Y., Chen, G., Potter, C. and Meentemeyer, R.K., 2019. Integrating multi-sensor remote sensing and
  species distribution modelling to map the spread of emerging forest disease and tree
  mortality. Remote sensing of Environment, 231, p.111238. doi: 10.1016/j.rse.2019.111238
- Hebblewhite, M. and Haydon, D.T., 2010. Distinguishing technology from biology: a critical review of
  the use of GPS telemetry data in ecology. Philosophical Transactions of the Royal Society B: Biological
  Sciences, 365(1550), pp.2303-2312. doi:10.1098/rstb.2010.0087
- Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.L. and Totland, Ø., 2009. How does climate warming
  affect plant-pollinator interactions?. Ecology Letters, 12(2), pp.184-195. doi: 10.1111/j.14610248.2008.01269.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
- Hoover, B.A., Miller, J.A. and Long, J., 2020. Mapping areas of asynchronous-temporal interaction in
- 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
- 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

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

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

Junker, R.R., Blüthgen, N., Brehm, T., Binkenstein, J., Paulus, J., Martin Schaefer, H. and Stang, M.,
2013. Specialization on traits as basis for the niche-breadth of flower visitors and as structuring
mechanism of ecological networks. Functional Ecology, 27(2), pp.329-341. doi: 10.1111/13652435.12005

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

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

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

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

979 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

983 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
- 985 Mayor, S.J., Guralnick, R.P., Tingley, M.W., Otegui, J., Withey, J.C., Elmendorf, S.C., ... Schneider, D.C.,
- 986 2017. Increasing phenological asynchrony between spring green-up and arrival of migratory birds.

987 Scientific Reports, 7(1), pp.1-10. doi:10.1038/s41598-017-02045-z

988 Memmott, J., Waser, N.M. and Price, M.V., 2004. Tolerance of pollination networks to species 989 extinctions. Proceedings of the Royal Society of London. Series B: Biological Sciences, 271(1557), 990 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.14610248.2007.01061.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

- 1000 Miller, J.A., 2012. Using spatially explicit simulated data to analyze animal interactions: a case study
- 1001 with brown hyenas in northern Botswana. Transactions in GIS, 16(3), pp.271-291. doi: 10.1111/j.1467-

1002 9671.2012.01323.x

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

Misra, G., Buras, A., Heurich, M., Asam, S. and Menzel, A., 2018. LiDAR derived topography and forest
stand characteristics largely explain the spatial variability observed in MODIS land surface
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

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

Morellato, L.P.C., Alberton, B., Alvarado, S.T., Borges, B., Buisson, E., Camargo, , ... Peres, C.A., 2016.
Linking plant phenology to conservation biology. Biological Conservation, 195, pp.60-72. doi:
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

Nilsson, C., Dokter, A.M., Schmid, B., Scacco, M., Verlinden, L., Bäckman, J., ... Liechti, F., 2018. Field
validation of radar systems for monitoring bird migration. Journal of Applied Ecology, 55(6), pp.25522564. 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

Oliver, T.H., Heard, M.S., Isaac, N.J., Roy, D.B., Procter, D., Eigenbrod, F., ... Proença, V., 2015.
Biodiversity and resilience of ecosystem functions. Trends in Ecology & Evolution, 30(11), pp.673-684.

1030 doi: 10.1016/j.tree.2015.08.009

1035

Oliver, R.Y., Ellis, D.P., Chmura, H.E., Krause, J.S., Pérez, J.H., Sweet, S.K, ... Boelman, N.T., 2018.
Eavesdropping on the Arctic: Automated bioacoustics reveal dynamics in songbird breeding
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

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

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

Pau, S., Wolkovich, E.M., Cook, B.I., Davies, T.J., Kraft, N.J., Bolmgren, K., ... Cleland, E.E., 2011.
Predicting phenology by integrating ecology, evolution and climate science. Global Change Biology 17,
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

- Peñuelas, J., T. Rutishauser, and I. Filella (2009), Phenology feedbacks on climate change, Science,
  324(5929), pp.887–888. doi:10.1126/science.1173004
- Peterson, A., Soberón, J., Pearson, J.R.G., Anderson, R. P., Martinez-Meyer, E., Nakamura, M. and
  Araújo, M. B. 2011. Ecological niches and geographic distributions (MPB-49). Princeton, NJ: Princeton
  University Press.
- Peterson, A.T., Soberón, J., Ramsey, J. and Osorio-Olvera, L., 2020. Co-occurrence networks do not
  support identification of biotic interactions. Biodiversity Informatics, 15(1), pp.1-10. doi:
  10.17161/bi.v15i1.9798
- Phillimore, A.B., Leech, D.I., Pearce-Higgins, J.W. and Hadfield, J.D., 2016. Passerines may be
  sufficiently plastic to track temperature-mediated shifts in optimum lay date. Global Change Biology,
  22(10), pp.3259-3272. doi: 10.1111/gcb.13302
- Pieretti, N., Farina, A. and Morri, D., 2011. A new methodology to infer the singing activity of an avian
  community: The Acoustic Complexity Index (ACI). Ecological Indicators, 11(3), pp.868-873. doi:
  1062 10.1016/j.ecolind.2010.11.005
- Ponti, L., Cossu, Q.A. and Gutierrez, A.P., 2009. Climate warming effects on the *Olea europaea Bactrocera oleae* system in Mediterranean islands: Sardinia as an example. Global Change Biology,
  15(12), pp.2874-2884. doi: 10.1111/j.1365-2486.2009.01938.
- Ponti, L., Gutierrez, A.P., Basso, B., Neteler, M., Ruti, P.M., Dell'Aquila, A. and Iannetta, M., 2013. Olive
  agroecosystems in the Mediterranean Basin: multitrophic analysis of climate effects with processbased representation of soil water balance. Procedia Environmental Sciences, 19, pp.122-131. doi:
  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

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

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

- Roberts, A.M., Tansey, C., Smithers, R.J. and Phillimore, A.B., 2015. Predicting a change in the order of
  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.,
- 1099 2009. Climate change effects on migration phenology may mismatch brood parasitic cuckoos and their
- 1100 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
- 1103 Sayer, E.J., 2018. The anatomy of an excellent review paper. Functional Ecology, 32(10), pp.2278-2281.
- 1104 doi: 10.1111/1365-2435.13207
- 1105 Schleuning, M., Fruend, J., Schweiger, O., Welk, E., Albrecht, J., Albrecht, M., ... Boehning-Gaese, K.,
- 1106 2016. Ecological networks are more sensitive to plant than to animal extinction under climate change.
- 1107 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.
- 1110 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
- 1112 sea turtles. Functional Ecology, 31(12), pp.2310-2319. doi: 10.1111/1365-2435.12930
- 1113 Schweiger, O., Biesmeijer, J.C., Bommarco, R., Hickler, T., Hulme, P.E., Klotz, S., ... Petanidou, T., 2010.
- 1114 Multiple stressors on biotic interactions: how climate change and alien species interact to affect
- 1115 pollination. Biological Reviews, 85(4), pp.777-795. doi: 10.1111/j.1469-185X.2010.00125.x
- 1116 Shonfield, J. and Bayne, E., 2017. Autonomous recording units in avian ecological research: current
- 1117 use and future applications. Avian Conservation and Ecology, 12(1). doi: 10.5751/ACE-00974-120114

- Silva, D.P., Gonzalez, V.H., Melo, G.A., Lucia, M., Alvarez, L.J. and De Marco Jr, P., 2014. Seeking the
  flowers for the bees: integrating biotic interactions into niche models to assess the distribution of the
  exotic bee species *Lithurgus huberi* in South America. Ecological Modelling, 273, pp.200-209. doi:
  10.1016/j.ecolmodel.2013.11.016
- Simmonds, E.G., Cole, E.F. and Sheldon, B.C., 2019. Cue identification in phenology: A case study of
  the predictive performance of current statistical tools. Journal of Animal Ecology, 88(9), pp.1428-1440.
  doi: 10.1111/1365-2656.13038
- de Souza Laurindo, R., Gregorin, R. and Tavares, D.C., 2017. Effects of biotic and abiotic factors on the
  temporal dynamic of bat-fruit interactions. Acta Oecologica, 83, pp.38-47. doi:
  10.1016/j.actao.2017.06.009
- Steinmetz, R., Seuaturien, N. and Chutipong, W., 2013. Tigers, leopards, and dholes in a half-empty
  forest: assessing species interactions in a guild of threatened carnivores. Biological Conservation, 163,
  pp.68-78. doi: 10.1016/j.biocon.2012.12.016
- Sullivan, B.L., C.L. Wood, M.J. Iliff, R.E. Bonney, D. Fink, and S. Kelling. 2009. eBird: a citizen-based bird
  observation network in the biological sciences. Biological Conservation, 142, pp.2282-2292. doi:
  10.1016/j.biocon.2009.05.006
- Tape, K.D. and Gustine, D.D., 2014. Capturing migration phenology of terrestrial wildlife using camera
  traps. BioScience, 64(2), pp.117-124. doi: 10.1093/biosci/bit018
- Thackeray, S.J., Henrys, P.A., Hemming, D., Bell, J.R., Botham, M.S., Burthe, S., ... Mackay, E.B., 2016.
  Phenological sensitivity to climate across taxa and trophic levels. Nature, 535(7611), pp.241-245.
  doi:10.1038/nature18608
- Terraube, J., Villers, A., Poudré, L., Varjonen, R. and Korpimäki, E., 2017. Increased autumn rainfall
  disrupts predator-prey interactions in fragmented boreal forests. Global Change Biology, 23(4),
- 1141 pp.1361-1373. doi: 10.1111/gcb.13408

- Theobald, E.J., Gabrielyan, H. and HilleRisLambers, J., 2016. Lilies at the limit: Variation in plantpollinator interactions across an elevational range. American Journal of Botany, 103(2), pp.189-197.
  doi: 10.3732/ajb.1500416
- Timberlake, T.P., Vaughan, I.P. and Memmott, J., 2019. Phenology of farmland floral resources reveals
  seasonal gaps in nectar availability for bumblebees. Journal of Applied Ecology, 56(7), pp.1585-1596.
  doi: 10.1111/1365-2664.13403
- Van de Pol, M., Bailey, L.D., McLean, N., Rijsdijk, L., Lawson, C.R. and Brouwer, L., 2016. Identifying the
  best climatic predictors in ecology and evolution. Methods in Ecology and Evolution, 7(10), pp.12461257. 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
- significance and consequences for primary consumers. Annual Review of Ecology and Systematics,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
- 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
- Virkkala, R., Heikkinen, R.K., Leikola, N. and Luoto, M., 2008. Projected large-scale range reductions of
  northern-boreal land bird species due to climate change. Biological Conservation, 141(5), pp.13431353. 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-

Visser, M.E., Caro, S.P., Van Oers, K., Schaper, S.V. and Helm, B., 2010. Phenology, seasonal timing and
circannual rhythms: towards a unified framework. Philosophical Transactions of the Royal Society B:
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
- Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., ... Heikkinen, R.K., 2013.
  The role of biotic interactions in shaping distributions and realised assemblages of species:
  implications for species distribution modelling. Biological Reviews, 88(1), pp.15-30. doi:
- 1173 10.1111/j.1469-185X.2012.00235.x
- Wolf, A.A., Zavaleta, E.S. and Selmants, P.C., 2017. Flowering phenology shifts in response to
  biodiversity loss. Proceedings of the National Academy of Sciences, 114(13), pp.3463-3468. doi:
  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
- avian brood parasite, the lesser cuckoo *Cuculus poliocephalus*. Global Ecology and Conservation, 22,
- 1179 p.e00976. doi: 10.1016/j.gecco.2020.e00976